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THE FLIGHT ACTIVITY OF HETEROPTERA

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With 3 Text-figures

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Introduction

Little quantitative information is available on the flight activity of Heteroptera. Large-scale migrations are well known in *Eurygaster integriceps* (Fedotov, 1947–55; Vodjdani, 1954), and Tischler (1937) has shown how various pentatomids move into hibernating sites in the autumn. The invasion, presumably by flight, of crops by species of *Lygus, Dysdercus* and other pest species is frequently recorded in the literature of applied entomology. Numbers of Heteroptera were recorded by Coad (1931), Glick (1939, 1957) and Freeman (1939, 1945), who trapped insects at various heights above the ground. Johnson and Southwood (1949) list Heteroptera caught in tow-nets between 50–4000 feet above ground level; they drew attention to the disproportionately large number of *Lygus rugulipennis* Poppius (= *Lygus pratensis* auctt., *vide* Southwood, 1956) compared with other Miridae. Accounts of the Heteroptera taken in light traps are given by Thomas (1938), Frost (1952) and Meurer (1956, 1957); the two last-named authors point out the great preponderance of male mirids and the absence from the catches of certain species abundant in the field. Brown (1954), Leston and Gardner (1953) and Leston (1953*a*, *b*, 1954) have given data on light trap catches of aquatic Heteroptera, in these cases entirely Corixidae.

Most of these studies have been either qualitative in their nature, for a short period or entirely confined to light traps, and none of the authors had the opportunity to relate in a quantitative way trap catches to adjacent field populations. The present author, therefore, welcomed the opportunity, afforded by the kindness of Dr. C. B. Williams and Dr. C. G. Johnson, to examine various light and suction trap catches, made in the grounds of Rothamsted Experimental Station, Harpenden, Hertfordshire, at different periods over the years 1947–56; the data from these catches form the main basis of the present paper.

The numbers of flying insects caught in traps, either light or suction, are a reflection of flight activity and population size; with light traps there is the additional complication of the insects' reaction to light.

With insects such as Lepidoptera and Diptera, in which flight is a repeated occurrence during a long adult flying life (*vide* Southwood and Johnson, 1957), it is possible to assume that the variation due to activity is represented by the differences between successive catches; this factor can then be eliminated and changes in population can be studied (Williams, 1940, 1951*b*). Even so, this method needs care in its application, and it is doubtful if it can be applied universally (Johnson, 1952). However, with Heteroptera, which are insects whose normal mode of locomotion is walking and which may perhaps fly for only part of their life, the trap population is a reflection of the flight activity of that part of the population which is currently able to fly. As Brown (1954) has shown with corixids, and Southwood and Johnson (1957) have suggested with certain beetles and bugs, almost all the individuals in populations may suddenly indulge in flight; once such explosive flights are over, although the general population in the area may remain almost as large, few, if any, will be caught in light or suction traps. Thomas (1938) gives what may be considered an example of such a flight in the males of *Asciodema obsoletum* (Fieber), in which 77 specimens (out of a four-year total of 158) were taken in one night. In

the present paper, therefore, attention is focused on the evidence of flight activity rather than on population changes.

Suction traps are considered to take a nearly random sample of the population of flying insects in their immediate vicinity (Johnson and Taylor, 1955), and in the present paper it is claimed that a comparison of the results of light and suction trap samples enables the effects of phototaxis and " catchability " to be separated from those of flight activity in light trap catches. Some idea of the differential flight activity of various species is obtained by a comparison of the numbers taken in a suction trap (No. 7) with the number swept and the number taken from the herbage with a suction apparatus (Johnson, Southwood and Entwistle, 1957) over the same period in the area immediately adjacent.

The nomenclature of the British species and of the families follows Southwood and Leston (1959).

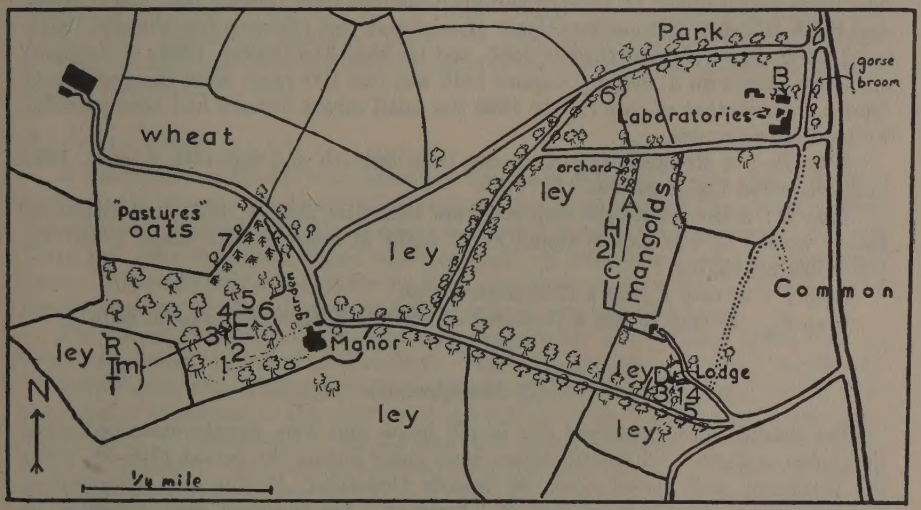

FIG. 1.—Sketch map of part of the grounds of Rothamsted Station, Harpenden, Herts., showing the positions of the various light traps (A–D, E_{1-6}, H, R, T_m and T) and suction traps (1–7) and the trees, crops or grass leys in their vicinity at the time of operation. (Trap R_D was in the same position as D.)

I. LIGHT TRAPS

(1) *The Traps*

During the years 1946–49 Dr. C. B. Williams ran three light traps at Rothamsted Experimental Station, Harpenden. The sources of light in these traps, known as Rothamsted traps, were 200-watt gas-filled tungsten filament bulbs. The design of the traps, which is described in detail by Williams (1948), allowed the bulb to be visible from the sides but not from above. Traps of a similar design were used for an intensive trapping experiment in 1949 and a single trap was run in 1955 and 1956.

In 1950 Dr. Williams compared the Robinson trap, described by Robinson and Robinson (1950), with the Rothamsted trap. The Robinson trap uses a mercury vapour bulb and therefore has a high ultra-violet content; its design is such that the bulb is visible from above, but it is not as efficient as the Rothamsted trap in catching slow flying insects. This experiment is described by Williams (1951*a*).

The position of all these traps is shown in figure 1, and their trapping periods and environs are indicated below. Unless otherwise stated, all are Rothamsted-type traps.

Trap A, 1946–49 : situated on a field path between a pasture, a mangold field and a small mixed orchard. This trap was in the same position as that used by Williams in 1933–36 (1939, 1940), and so a direct comparison may be made between the species taken in trap A in the present study and those recorded by Thomas (1938), who details the Heteroptera collected from 1933–36.

Trap B, 1946–49 : on the roof of Rothamsted main laboratory building ; many trees, especially lime (*Tilia*), are in the immediate vicinity.

Trap C, 1946 *and* 1947 : in a short grass enclosure between arable and pasture fields ; about 200 yards from trap A, but in the more exposed situation.

Trap D, 1948–49 : in Rothamsted Lodge garden, at the edge of a small lawn and adjacent to ornamental conifers and some small sallows (*Salix capraea*) ; other trees, chiefly oak (*Quercus*), were about 20 yards distant.

Traps E_1–E_6 : six traps run during July, 1949 in Rothamsted Manor wood. The wood covers about 14 acres of various deciduous trees (mostly oak, elm (*Ulmus*) and birch (*Betula*)) and conifers (larch (*Larix*) and yew (*Taxus*)) (*see* French, 1951).

Trap H, 21*st July*–31*st October*, 1955, *and* 1*st May*–31*st October*, 1956 : a Rothamsted-type trap with a mercury vapour bulb was run 100 yards from the position of trap A towards that of trap C. In 1950 the small mixed orchard had been replaced by hard tennis courts.

Trap R_D : a Robinson-type trap run from 3rd–7th and 9th–14th August, 1950 in Rothamsted Lodge garden.

Trap R : a Robinson-type trap run from 16th–31st August, 1950 in Rothamsted Manor wood ; it was moved round every night in rotation with traps T and T_m (*see* Williams, 1951*a*).

Trap T : as trap R, but a Rothamsted type.

Trap T_m : as trap R, but a Rothamsted type with a mercury vapour bulb.

(2) *Identifications*

The catches were preserved dry in pill boxes and were mostly examined some time after capture. All identifications were made during the period 1948–51, when the taxonomy and identification of various *Orthotylus*, *Psallus* and *Macrolophus* was uncertain. A certain amount of " lumping " has therefore been necessary in these genera. The more precise identifications given for the species from traps E_1 and E_6 and for *Lygus* have been recently verified. The author identified only the early captures from trap H ; the great majority were determined by Dr. G. G. E. Scudder, who has generously made these records available.

(3) *Comparison between Years*

(a) *Monthly Totals*

Almost all the Heteroptera taken in light traps are caught between June and September ; these are, of course, the months when mirids, which make up the majority of the catch (p. 191), are most abundant in the field. The monthly totals of all species for the four years are given in Table I, which shows that the distribution of the total catch in the various months differs from year to year. In 1946, 1947 and 1949, the catches were spread over the whole " summer " period, with the highest figures in July and August. From the incomplete data, 1955 would appear to be similar, although the September catch was probably larger than usual. In 1948 the total was of the same order as in 1949 and 1956, but the majority of the catch occurred on five nights in late July (26th–30th, catches respectively : 64, 256, 287, 204 and 137).

Thus in 1948 only very small samples were taken of the population of flying Heteroptera at periods other than the end of July, and this is reflected in the low

TABLE I.—*The monthly distribution of all Heteroptera taken in light traps in various years*

(*1946-49, based on three traps, 1955-56 on one trap.*)

Year	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1946	.	.	.	.	1	9	235	366	50	6	.	.	667
1947	.	.	.	.	.	213	796	738	283	5	.	3	2038
1948	.	.	1	2	8	17	1069	156	44	2	2	.	1301
1949	4*	.	.	.	.	115	476	524	204	19	4	5	1351
1955	.	.	.	.	.	.	87†	511	309	4	.	.	911
1956	.	.	.	.	1	5	288	230	15	.	.	.	539

* Taken in January, 1950; † from 21st to 31st July only.

indices of diversity (Table III) for all traps in this year compared with 1947 and 1949 when "reasonable samples" were taken throughout the season. An explanation for the different distribution of the catch in the various years in terms of climate will be given later (p. 183).

(b) *Species Totals*

A comparison of the six most abundant species in each of the nine years in which a trap was in the same position (Table II) shows that three species, *Lygus rugulipennis*, *Adelphocoris lineolatus* and *Megalocoleus molliculus* were in this category in all nine years, and over the whole period together made up almost half (48 per cent.) total catch. Although only amongst the six most abundant species in five years, *Orthotylus flavosparsus* was the fourth most numerous species over the nine years.

The species make-up of the light trap samples for the different years may be compared, using the index of diversity. This was devised by Fisher, Corbet and Williams (1943) and Williams (1947); the higher the index, the higher the ratio of the number of species to the number of individuals in the population, *i.e.* the more diverse it is. Different-sized samples from the same population will have the same index of diversity. Two populations may have the same index of diversity, although differing qualitatively in their constitution; if they do differ in this way then the index of diversity of their combined samples will be greater than their individual indices.

A comparison may be made between the species taken by Thomas (1938) during the period 1933–36 and during the present study (1946–49) in the same trap (A). The approximate indices of diversity (uncertainty over the number of species of *Psallus* and *Orthotylus* precludes an exact test) for the two periods are: 1933–36, 16 ($S = 1486$, $N = 74$) and 1946–49, 15 ($S = 2104$, $N = 76$); but for the whole eight years it is 18 ($S = 3590$, $N = 95$). As the latter value is greater than those for the separate periods (which are also greater than those of the individual years), it may be concluded that the population sampled in one year was not the same as that sampled in the next. These qualitative changes in fauna can be examined in detail; Thomas (1938) recorded 17 species that were not taken in 1946–49. Five of these were corixids whose disappearance may be associated with the draining of a nearby pond; three were associated with Scots pine (*Pinus sylvestris*) and a row of these trees, 800 yards away, was cut down in 1944. A further seven species, each represented by only one individual in 1933–36, *Calocoris fulvomaculatus*, *Macrolophus nubilis*, *Dicyphus epilobii*, *Neomecomma bilineatus*, *Malacocoris chlorizans*, *Heterotoma meriopterum* and *Leptopterna dolabrata*, were absent in 1946–49, and it is possible that the vegetational changes account for the disappearance of the first four species from the immediate vicinity of the trap. The absence of *Lygocoris spinolae* (2 individuals) and *Stalia major* (7 individuals) from the 1946–49 samples is unlikely to be due to such changes. None of these species were taken in the trap in 1955 or 1956.

Twenty species (excluding taxonomic changes) were found in 1946–49 that had

TABLE II.—*The most abundant Heteroptera in nine years light trap catches in the same position*

(The actual catches followed by the percentage of the total catch are given for the six most abundant species in each year ; the figures in italics are the catches of these species in the other years when they were not amongst the six most abundant. Data for 1933–36 *are taken from Thomas* (1938).

Species	1933	1934	1935	1936	1946	1947	1948	1949	1956	Total all years
Lygus rugulipennis Popp.	81/22·1	70/14·1	133/28·7	14/9·1	35/18·0	252/34·1	310/56·0	81/13·2	432/79·0	1412/34·0
Adelphocoris lineolatus (Goeze)	71/18·9	57/11·5	42/9·1	36/23·5	76/39·0	80/10·8	56/10·1	153/24·9	12/2·2	583/14·1
Megalocoleus molliculus (Fall.)	26/6·9	50/10·1	148/32·0	13/8·5	9/4·6	43/5·8	61/11·0	40/6·5	21/3·9	411/9·9
Orthotylus flavosparsus (Sahlb.)	*8*	42/8·5	*1*	*2*	*6*	169/22·8	17/3·1	106/17·2	27/4·6	378
Orthops kalmi (L.)	28/7·4	25/5·1	27/5·8	*5*	8/4·1	50/6·8	18/3·2	57/9·3	20/3·7	238
Asciodema obsoletum Fieber	39/10·4	144/29·1	*5*	*0*	*5*	*3*	*4*	*12*	*0*	212
Stenotus binotatus (Fab.)	32/8·5	*13*	12/2·6	23/15·0	*2*	*13*	*10*	*9*	*0*	114
Stenodema calcaratum (Fall.)	*3*	*4*	*17*	15/9·8	*6*	*3*	14/2·5	*2*	*3*	67
Nabis ferus (L.)	*1*	*2*	*5*	*0*	*0*	*15*	*2*	38/6·1	*0*	63
Trignotylus ruficornis (Geoff.)	*0*	*5*	*1*	*1*	*0*	*17*	*1*	*3*	4/0·7	32
Phytocoris varipes Boheman	*0*	*0*	*0*	*0*	*2*	21/2·8	*2*	*4*	*1*	30
Blepharidopterus angulatus (Fall.)	*0*	*0*	*5*	*4*	10/5·1	*8*	*3*	*0*	*0*	30
Orthops cervinus (H.–S.)	*5*	*0*	*0*	*1*	12/6·2	*7*	*1*	*3*	*1*	30
Pachylops bicolor (Doug. and Scott)	*0*	*8*	15/3·2	*0*	*0*	*0*	*0*	*0*	*0*	23
Plesiodema pinetellum (Zett.)	*0*	*0*	*0*	15/9·8	*0*	*1*	*0*	*0*	*0*	16
Total catch in all species	376	494	463	153	196	740	554	615	539	4130
Six most abundant as percentage total catch	74·2	78·4	81·4	75·7	77·0	83·1	85·9	77·4	94·1	

not been recorded by Thomas (1938); 12 of these were represented by only a single specimen, and their absence from 1933–36 samples could have been due to the smaller size of the latter; the same applies to *Lyctocoris campestris* (associated with hay and straw stacks), two specimens of which were taken. The seven remaining species, with their host plants and the numbers caught were: *Pentatoma rufipes* (trees, especially oak, 8); *Deraeocoris scutellaris* (? hazel, 10); *Oncotylus viridiflavus* (knapweed, *Centaurea nigra*, 6); *Campylomma verbasci* (apple, 8); *Phytocoris reuteri* (trees, especially apple, hawthorn and oak, 9); *P. varipes* (grasses, other waste land plants, 29); *Polymerus nigritus* (goosegrass and other bedstraws, 5). *C. verbasci* was first discovered in Britain in 1938 and was increasing its range at this time (Southwood, 1957); *D. scutellaris* is a rare species and its occurrence has already been discussed (Southwood, 1950); the host plants of *O. viridiflavus* and *P. nigritus* may have increased since 1936. The absence of the other species, more especially *Phytocoris varipes*, from the 1933–36 catches cannot be explained. Three of these species, *L. campestris*, *O. viridiflavus*, and *Polymerus nigritus* were present in the 1955–56 catches. The removal of the mixed orchard and its associated hedge in 1950 no doubt accounts for the absence of arboreal species in the latest trap catches (Table XVII).

(4) *Comparison between Traps*

A comparison between the catches of traps running at the same time in a given area will give an indication of the extent to which the population of flying Heteroptera is uniform over that area and, incidentally, some measure of flight range (see p. 216).

(a) *Three Traps in Different Situations*

From 1946–49 three traps, either A, B and C, or A, B and D, were run at Rothamsted Experimental Station; their positions are described on p. 176 (fig. 1). An examination of the catches shows that each trap sampled a different population which was related to its immediate environs. The first evidence for this was obtained from a comparison of the indices of diversity of the traps (Table III); these show

TABLE III.—*The catches of Heteroptera of four differently positioned light traps in terms of number of individuals (N), number of species (S), and index of diversity (α)*

	1946			1947			1948			1949		
Trap	*N*	*S*	α	*N*	*S*	α	*N*	*S*	α	*N*	*S*	α
A	196	29	9	740	44	10	554	33	8	615	37	8·5
B	208	26	8	503	48	13	392	32	8·5	404	41	12
C	264	19	4	795	28	5·5	.	.	.	.	.	.
D	.	.	.	.	.	.	355	26	6·5	332	36	10
All traps	668	41	10	2038	60	11·5	1301	46	9	1351	60	13

that the variation between traps in any one year is too great to permit the assumption that all the traps were sampling the same population. This view is reinforced by the combined indices of diversity for all traps in any one year, which in 1946, 1947 and 1949 were greater than any of the values for individual traps.

Trap C was 200 yards from trap A, yet its index of diversity is about half that of trap A (error of index at this level 12 per cent.); these traps, therefore, although relatively close, are sampling different populations. Traps B and D were much further from A and each other, and thus it may be assumed that, even though the values for the index of diversity are not significantly different, the populations are likely to differ. Distinction may be expected to show itself both quantitatively in

TABLE IV.—*A comparison of the total number of individuals of the major species of Heteroptera grouped according to host plant in four light traps in different positions.* (*Arboreal species*: Psallus *spp.*, Blepharidopterus angulatus, Orthotylus *spp.* (*subgenus* Orthotylus *less* adenocarpi *species group*), Phytocoris *spp.* (*except* P. varipes) *and* Orthops cervinus. *Weed species*: Megalocoleus molliculus. Orthotylus flavosparsus, Lygus rugulipennis, Adelphocoris lineolatus *and* Orthops kalmi. *Grass species*: Nabis ferus, Phytocoris varipes, Stenotus binotatus, Trignotylus ruficornis *and* Stenodema calcaratum)

	Arboreal species		Weed species		Grass species	
Trap	1946–47	1948–49	1946–47	1948–49	1946–47	1948–49
A	71	58	728	899	79	85
B	201	292	425	399	49	27
C	28	.	908	.	75	.
D	.	116	.	437	.	68

differing populations of the common species and qualitatively in the species list for each trap. Each of these aspects is now considered in turn.

An examination of Table IV shows that trap B (on the roof of a building, near trees) caught a large number of individuals of the arboreal species, fewer weed species than A or C, and fewer grass species than any other trap. Trap C (between fields and pastures) took most weed species and large numbers of grass Heteroptera. As would be expected from their situations, traps A and D are intermediate between B and C.

During the four years 12 species were taken only in trap A; all, except the apple capsid, *Plesiocoris rugicollis* (2 specimens), and the ubiquitous but usually flightless *Nabis rugosus* (3 specimens), were represented by a single specimen. Fourteen species were confined to trap B; 12 of these were taken in one year only and were represented by less than six individuals; these were: six species of corixid (Brown, 1954), five arboreal species and one (*Reduvius personatus*) associated with buildings. Two species were taken in more than one year; there were *Pachylops bicolor* in all four years and *Lopus decolor* in 1946 and 1949. Both these species occur on Harpenden Common (fig. 1), the former on gorse (*Ulex europeus*) and the latter amongst the short dry grass. Neither species was found in the grounds of Rothamsted Experimental Station itself during extensive collecting by the present author.

Traps C and D each ran for only two years; each trap had two unique species represented by single specimens.

(b) *Six Traps in the Same Wood*

During July, 1949 six light traps (E_1–E_6) were run in Rothamsted Manor wood. An account of the Lepidoptera caught in these traps, with details of their positions and surroundings, is given by French (1951). Trap 1 was in a fairly open position in a broad mowed grass-ride, trap 2 about 30 yards away in a small glade, traps 3 and 4 were in similar positions on a woodland path 25 yards apart, and traps 5 and 6 in denser woodland 40 yards apart.

Heteroptera taken in the various traps are listed in Table V and the index of diversity has been calculated for each trap using Williams' (1947) diagrams. It will be seen that the combined index for all traps and the indices for four of the individual traps are of the same order; the error of the estimate of the index at this level is about 25 per cent. so that the difference between the indices of traps 4 and 5 and those of traps 1 and 3 is just significant. The low index for trap 4 is due to the large number of *Pentatoma rufipes* taken. It would appear, therefore, that the traps are sampling the same general population with certain local variations.

TABLE V.—*The Heteroptera taken in six light traps running in Rothamsted Manor wood in July*, 1949

	1	2	3	4	5	6	All traps ♂	All traps ♀
Pentatoma rufipes (L.)	4	11	10	28	9	4	64	2
Nabis ferus (L.)	3	.	.	.	.	.	3	.
Anthocoris nemoralis (Fab.)	.	.	.	.	1	.	.	1
Megalocoleus molliculus (Fall.)	7	3	.	.	.	.	9	1
Macrotylus solitarius (Mey.-Dür.)	23	2	2	1	.	1	28	1
Psallus perris Wagner	1	.	.	.	.	.	1	.
P. diminutus (Kirsch)	.	.	.	1	.	.	.	1
P. salicellus (H.–S.)	20	3	1	11	1	.	22	14
Plagiognathus arbustorum (Fab.)	1	.	2	.	.	.	3	.
*Macrolophus**	2	3	2	3	2	2	13	1
Dicyphus epilobii Reuter	1	.	.	.	.	.	.	1
D. errans (Wolff)	2	.	4	.	.	.	6	.
Campyloneura virgula (H.–S.)	.	4	.	2	1	2	.	9
Blepharidopterus angulatus (Fall.)	2	.	1	.	.	.	2	1
Orthotylus viridinervis (Kirsch)	.	.	1	.	.	.	1	.
O. marginalis Reut.	4	.	2	6	5	3	9	11
O. nassutus (Fab.)	2	.	.	2	.	.	4	.
O. ochrotrichus (Fieb.)	3	.	6	6	9	4	20	8
O. prasinus (Fall.)	.	.	.	1	.	.	1	.
O. adenocarpi (Perris)	1	.	.	.	.	.	1	.
O. virescens (Doug. and Scott)	2	1	1	.	.	.	3	1
O. flavosparsus (Sahlb.)	1	.	.	.	.	.	1	.
O. diaphanus (Kirsch)	1	.	3	.	.	.	4	.
Neomecomma bilineatus (Fall.)	1	.	.	.	.	.	1	.
Lygus rugulipennis Popp.	1	.	.	.	.	.	1	.
Orthops cervinus (H.–S.)	25	2	4	2	.	1	25	9
O. kalmi (L.)	2	.	.	.	.	.	2	.
Lygocoris pabulinus (L.)	4	1	.	3	.	1	.	9
L. viridis (Fall.)	.	.	.	2	.	.	1	1
L. lucorum (May.-Dür.)	.	1	.	.	.	.	.	1
Calocoris norvegicus (Gmelin)	.	.	1	.	.	1	2	.
Adelphocoris lineolatus (Goeze)	1	1	3	2	1	.	6	2
Stenotus binotatus (Fab.)	.	.	1	2	.	.	3	.
Phytocoris tiliae (Fab.)	.	1	1	.	.	.	2	.
P. dimidiatus (Kirsch)	.	2	.	.	.	.	1	1
P. longipennis Flor	.	3	.	1	1	.	4	1
P. reuteri Saunders	.	.	4	.	3	.	5	2
P. ulmi (L.)	1	1	1	.	.	.	1	2
P. varipes Boheman	2	.	1	.	1	2	6	.
Stenodema calcaratum (Fall.)	2	.	.	.	.	.	1	1
Trignotylus ruficornis (Geoff.)	2	1	.	.	.	.	2	1
							258	82
Total individuals	121	40	51	73	34	21	340	
Total species	28	16	20	16	11	10	41	
Index of diversity	12	10	12	6	6	8	11	

* Since these identifications were made British *Macrolophus* have been shown to belong to two species. Both are known to occur in this wood, but unfortunately the material was no longer available for fresh determinations to be made in the light of this revision.

An examination of the species pattern in Table V confirms this: trap 1, for example, took certain non-woodland species such as *Nabis ferus*, *Megalocoleus molliculus*, *Orthotylus flavosparsus*, *Lygus rugulipennis* and *Orthops kalmi*; this is consistent with its position. Large numbers of *Orthops cervinus*, *Macrotylus solitarius* and *Psallus salicellus* were found in this trap; in the case of the two latter the well-developed shrub and undergrowth layer (including their host plants, hedge wound-

wort, *Stachys sylvatica*, and bramble, *Rubus* agg.) was no doubt a contributing factor. The occurrence of the non-woodland *Adelphocoris lineolatus* in five of the six traps is a perhaps significant exception to the general conclusion that populations of a species occur in the proximity of the traps in which they were taken.

Traps 1–4 were in more open woodland and therefore with more ground cover and varied vegetation than traps 5 and 6; the two latter caught fewer individuals and, except in comparison with trap 4, had lower indices of diversity. It may be concluded that the trap catches reflect the Heteroptera present in their immediate neighbourhood, and that the similar indices of diversity are a reflection of the general uniformity of the habitat. It is noteworthy that the highest catches of Lepidoptera were in traps 4 and 5 (French, 1951).

(c) *Different Types of Traps*

In August, 1950 Williams (1951*a*) carried out an experiment to compare the relative efficiency of the Rothamsted-type trap fitted with a gas-filled tungsten filament bulb (T), the new Robinson mercury vapour light trap (R) and a Rothamsted-type trap with a mercury vapour bulb (T_m). There were three positions and the traps were moved round every night so that there should not be any bias due to position.

(i) *Total numbers.*—The details of the catches of terrestrial Heteroptera are given in Table VI with a summary of Brown's (1954) data on the corixids. Although the figures are rather small, they do show definitely that a higher catch was obtained by the Robinson trap; the figures for trap T_m would seem to suggest that this was due more to the " open top design " than to the mercury vapour light source.

The increase in numbers in the Robinson trap is even more striking in the Corixidae (*see also* Brown, 1954). High catches of corixids were also obtained by trap R_D, a

TABLE VI.—*The Heteroptera taken in different types of light traps in August*, 1950

Traps R_D and R, a Robinson mercury vapour trap; traps T_m, Rothamsted trap with mercury vapour bulb; trap T, a Rothamsted trap with tungsten bulb.

	R_D		R		T_m		T	
	♂	♀	♂	♀	♂	♀	♂	♀
Pentatoma rufipes (L.)	3	.	10	.	2	.	.	1
Anthocoris nemorum (L.)	.	.	.	1	1	.	.	1
Psallus salicellus (H.-S.)	1	1	1	.	.	.	.	.
Megalocoleus molliculus (Fall.)	22	.	.	.	.	.	.	.
Macrotylus solitarius (Mey.-Dür.)	1	.	.	.	.	.	.	.
Oncotylus viridiflavus (Goeze)	1	.	.	.	.	.	.	.
Blepharidopterus angulatus (Fall.)	.	.	1	.	.	.	.	.
Malacocoris chlorizans (Pans.)	.	.	1	.	.	.	.	.
Pachylops bicolor (Doug. and Scott)	1	.	.	.	.	.	.	.
Orthotylus flavosparsus (Sahlb.)	3	.	.	.	.	1	.	.
Lygus rugulipennis Popp.	27	4	2	.	.	.	.	.
Orthops cervinus (H.-S.)	1	.	3	1	1	.	2	.
Lygocoris pabulinus (L.)	2	.	.	1	.	.	.	.
L. viridis (Fall.)	1	.	.	.	.	.	.	.
Adelphocoris lineolatis (Goeze)	7	.	2	.	1	.	1	.
Stenotus binotatus (Fab.)	1	.	.	.	.	.	.	.
Phytocoris tiliae (Fab.)	.	.	1	.	.	.	1	1
P. varipes Boheman	2	.	.	.	.	.	.	.
Stenodema calcaratum (Fall.)	2	.	.	.	.	.	.	.
Trignotylus ruficornis (Geoff.)	1	1	1	.	.	.	.	.
Total—each sex	76	6	22	3	5	1	4	3
Total—both sexes	82		25		6		7	
Corixidae (Brown, 1954)	492		755		5		1	

Robinson-type trap operated during the first half of August, 1950 (Table VI); there was no comparable Rothamsted-type trap nearby at the time, but trap D had run in the same position throughout 1948, 1949 and until May, 1950, and over the whole of this period had taken only one corixid. Meurer (1956, 1957) has published results from a Robinson-type trap operated in Holland. In 1954 there were 17 corixids out of a total catch of 118 Heteroptera, and in 1955 there were 893 out of a total catch of 1498. There is thus obviously considerable variation from year to year, but the proportion of corixids, even in 1955, was higher than that in Rothamsted-type traps. Leston and Gardiner (1953) and Leston (1953*a*, *b*; 1954) also record numbers of corixids from an open-top mercury vapour light trap.

In conclusion, the Robinson type of trap catches somewhat higher numbers of terrestrial Heteroptera and far higher numbers of Corixidae than does the Rothamsted-type trap. The increase appears to be due more to the design than to the type of light source. This is in accord with the findings of Williams (1951) and Williams, French and Hosni (1955) that insects that fly fairly swiftly rather than flutter or hover are taken in larger numbers in the Robinson trap. Further evidence that ultra-violet is not the cause of the increase comes from the work of Frost (1953), who compared the catches of insects by black (*i.e.* emitting only ultra-violet light invisible to man) and white (*i.e.* normal) lamps of equal wattage. He found that, in contrast with most insects, more Heteroptera were taken in the traps with white lamps (1828 : 289).

As Popham (1942) has shown that corixids are attracted to a bright object, it seems probable that, like many aquatic beetles, they may fly almost vertically down on to any shining surface—in nature, of course, this would always be water. They are thus particularly susceptible to capture by the Robinson-type traps that are open above, and in this case the trap may truly be said to attract the insect (*c.f.* Robinson, 1952).

(ii) *Sex ratio.*—From Table VI it would appear that the ratio of males to females is rather higher in the traps with a mercury vapour-light-source than in those with the tungsten filament bulb. The ratio in the former case is 7·3 : 1; a more reliable figure for tungsten filament trap catches is obtained from the four years of traps, A, B, C and D, where the ratio is 5·5 : 1 (4401 : 798). Thus the increase in the numbers of terrestrial Heteroptera (mostly mirids, *see* pp. 205–12) in the Robinson trap compared with the Rothamsted trap is not distributed equally between the two sexes, but accentuates the already heavy preponderance of males (*see* p. 192).

With the Corixidae a combination of Thomas's (1938) and Brown's (1954) data gives 40 females to 15 males in the Rothamsted-type traps, and 624 to 628 in the open top Robinson traps. Here again the Robinson-type trap increases the proportion of males, in this case leading to equality in numbers as females are dominant in Rothamsted trap catches.

(5) *The Effect of Climate on Flight Activity*

The effect of various climatic factors on the size of the catch of total insects and of Lepidoptera alone has been analysed in detail by Williams (1940, 1951*b*). He described techniques, including the running mean, by which it is possible to separate the longer-term changes due to population fluctuations, from the short-term changes due to activity. Activity can be considered as represented by the departures from the running means. The use of the running mean has, however, the disadvantage that it considerably reduces, and makes difficult to assess, the number of degrees of freedom available for the calculation of the significance of statistical relationships between activity and various climatic factors. This is especially serious where, as in the present work, there are altogether less data available, and for this reason the original data with the catch figures transformed to log $(n + 1)$ have also been used

TABLE VII.—*A comparison of the climatic factors on various nights with high and low catches of Heteroptera in the light traps in* 1947

	High catch nights		Low catch nights
Number of nights	20		18
Highest number of Heteroptera/night	212		1
Lowest " " " "	31		0
Maximum temperature—highest value (°F.)	86·9		74·3
" " —lowest value (°F.)	71·3		54·1
" " —mean (°F.)	78·5		62·2
" " —"*t*"		(2·88)	
Minimum temperature—highest value (°F.)	63·2		59·1
" " —lowest value (°F.)	52·9		42·5
" " —mean (°F.)	55·8		49·6
" " —"*t*"		(0·59)	
Grass minimum temperature—highest value (°F.)	60·6		58·2
" " " —lowest value (°F.)	40·5		40·0
" " " —mean (°F.)	55·0		47·9
" " " —"*t*"		(1·34)	
Rainfall—mean (inches)	0·01		0·04
Wind—mean (Beaufort scale)	1.75		2.5
Barometric pressure, mid-day mean (mm. Hg)	30·11		29·98
" " mid-night mean (mm. Hg)	30·08		29·96

in many calculations. Williams (1940, 1947) gives an account of the value of the logarithmic transformation for such data.

A preliminary idea of the relationships between climate and catch size can be obtained by the selection of nights of high and low catch and a comparison of their climate. Table VII summarises such a comparison for 1947, between 25th June and 21st September; high catches were arbitrarily taken to be above 30 and low catches one or zero. The means of the various climatic factors have been calculated and the significance of the difference between the temperature means of the two groups of nights tested by the "*t*" test. It will be seen that the differences between the means for the other factors are only slight, although nights of high catch have a tendency for higher barometric pressure, less rain and less wind, than nights of low catch; it must be remembered, of course, that these climatic factors are themselves related and associated in these groups.

The means of the maximum temperatures differ significantly (probability 0·01), but of the minimum temperatures and grass minimum temperatures are not significant. This is remarkable, for Williams (1940) found that minimum temperature had a greater effect on the catches of total insects and of Lepidoptera than the maximum temperature. As Williams pointed out, all these measurements of climate are related to one another and a detailed consideration of their relationship is given in his paper. However, the maximum temperature usually occurs in the early afternoon and the minimum temperature just before dawn; thus, as the minimum temperature is closest to the mean of the night, one might expect *a priori* that this would be most closely correlated with the catch.

The relationship between maximum and minimum temperature and the catch of Heteroptera has been examined more closely by the calculation of correlation and regression coefficients for various sets of data (Table VIII). There are seven independent sets of correlations which measure the degree of association between two factors; in six of these the correlation coefficient for the relationship with maximum temperature has the higher coefficient, and therefore it is concluded that the maximum temperature has a greater effect on the catch than the minimum.

The regression coefficient for the equation of total catch on maximum temperature for the various periods in the five years 1946–49 and 1956 (a total for 340 nights catches) is 0·0612, which means that the catch is doubled for a rise in maximum

TABLE VIII.—*Correlation and regression coefficients for light trap catches of Heteroptera and temperature (* significant at 5 per cent. level, ** significant at 1 per cent. level, *** significant at 0·1 per cent. level)*

			Catch (log n + 1) on temperature				Deviations from 5-day running mean. Catch on maximum temperature	
			Minimum temperature		Maximum temperature			
Catch	Year	Period	Correlation	Regression	Correlation	Regression	Correlation	Regression
Total Heteroptera	1946	23.vii–22.viii	.	.	+0·326	0·0142	.	.
	1947	22.vi–22.ix	+0·391***	0·0502	+0·628***	0·0534	+0·657	0·0803
		22.vi–22.vii	+0·124	0·0172	+0·743***	0·0678	+0·448	0·0417
		23.vii–22.viii	+0·739***	0·0760	+0·710***	0·0761	+0·174	0·0272
		23.viii–22.ix	+0·355*	0·0379	+0·359*	0·0380	+0·318	0·0423
	1948	23.vii–22.viii	+0·402*	0·0660	+0·816***	0·0709	+0·347	0·00302
	1949	22.vi–22.ix	+0·686***	0·0753	+0·618***	0·0572	.	.
		22.vi–22.vii	+0·261	0·0911	+0·653***	0·0574	.	.
		23.vii–22.viii	+0·529**	0·0519	+0·750***	0·0551	+0·419	0·0278
		23.viii–22.ix	+0·623***	0·0709	+0·682***	0·0797	.	.
	1956	22.vi–22.ix	.	.	+0·388***	0·0482	+0·391	0·0422
		22.vi–23.vii	.	.	+0·478**	0·0508	+0·431	0·0497
		22.vii–23.viii	.	.	+0·308	0·0202	+0·344	0·0493
		22.viii–23.ix	.	.	+0·406*	0·0182	+0·488	0·0288
Lygus rugulipennis	1947	22.vi–22.ix	.	.	+0·578***	0·0463	.	.
		22.vi–22.viii	.	.	+0·632***	0·0483	.	.
		23.viii–22.ix	.	.	+0·393*	0·0368	.	.
Total Heteroptera	1946–49 1956	As above	.	.	+0·6460***	0·0612	.	.

temperature of 4·9° F. (= 2·7° C.). The regression line is shown graphically in figure 2, from which it will be seen that the catch is generally zero with maxima of 59° F. or less, and only rises steadily and steeply above 75° F. (at which temperature ten bugs are generally caught).

The line for the regression of total catch on minimum temperature is naturally to the left of that for maximum ; in 1949 the association between minimum temperature and catch was closest (Table VIII) and the regression line has therefore been drawn for that year (fig. 2). It will be seen that it rises more steeply than that for temperature ; zero catch corresponds to a minimum temperature of 41° F. The relation of catch to maximum temperature has been analysed in the case of a single species, *Lygus rugulipennis* (Table VIII), and the coefficients are of the same order as those for total catch.

Because the number of degrees of freedom are but one-fifth of that of the original data, the correlation coefficients for the deviations from the five day running mean are unfortunately seldom " significant "; they are, however, not greatly dissimilar from those of Williams (1940). The regression coefficients are, in general, lower than those for the original data, which means that a greater rise in temperature is necessary to produce a doubling of the activity than to produce a doubling of the catch—some part of the increase in catch being due to an increase in the flying population.

It can be concluded that very little flight activity will occur when the maximum temperature is below 70° F. (= 21° C.), and large catches will only occur on days with

maxima of 75° F. (= 24° C.) or more. Now certain differences already noted (p. 176) between the distribution of catches in 1947 and 1949 on the one hand and 1948 on the other, are entirely explained if the distribution of days with a maximum temperature of 75° F. or more is considered. In 1948 such days were 25th–31st July and 1st August and 9th September, and the only large catches of Heteroptera occurred on 26th–31st July. In 1947 and 1949, in contrast, there were respectively 39 and 38 days, between mid-June and late September, with maxima of 75° F. or more, and " large " catches occurred on many nights from June to September.

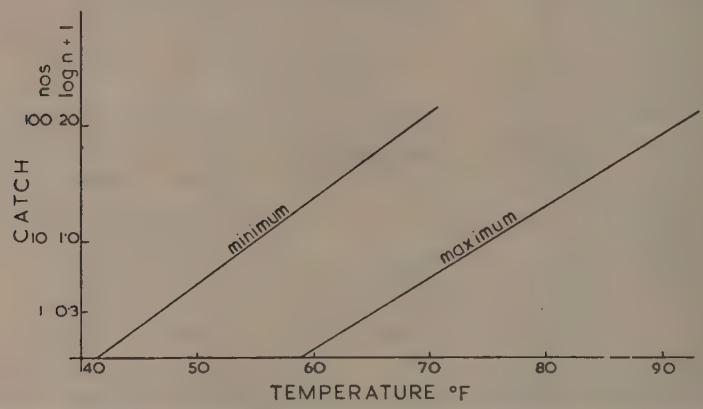

Fig. 2.—The regressions of the catch of Heteropera in light traps on maximum and minimum temperature. (Maximum temperature based on 1946–49 and 1956, minimum on 1949.)

II. Suction Traps

(1) *The Traps*

Suction traps were devised by Johnson and Taylor to take a sample of the absolute population of airborne insects. Details of the design and performance of each type of trap are given by Johnson (1950), Taylor (1951, 1955) and Johnson and Taylor (1955).

The traps from which the Heteroptera have been identified are listed below ; their positions are shown in figure 1.

Trap 1.—A 6-inch trap of the Vent-Axia type was operated in the garden of Rothamsted Lodge from 2nd June to 26th November, 1947.

Trap 2.—An 18-inch propeller-type trap was operated from 23rd June to 13th November, 1947 on the edge of a grass enclosure next to a pasture. This trap was about 20 yards from light trap C, which was working at the same time. An account of the aphids taken is given by Johnson and Eastop (1951).

Trap 3.—This was an 18-inch propeller-type trap situated in Rothamsted Lodge garden within 30 yards of the position formerly occupied by light trap D. In 1950 there was a single trap 5 feet above the ground ; it was emptied just before dusk and just after dawn, so that the day and night catches were segregated. The Heteroptera were identified for the period 18th June–13th August inclusive. In 1953 two traps were placed about 5 yards from the above site and operated from 1st March until December, one 5 feet above the ground level as before, and the other (trap 3T) at about 30 feet above it. Both traps were sampled for two periods, one from 12 noon to 2 p.m., taking the " day catch ", and a second from a quarter of an hour after sunset until midnight, taking the night catch. All the Heteroptera caught were identified. Further details of trap 3 for 1950 are given by Singh (1952), and of its use in 1953 by El-Ziady (1954).

TABLE IX.—*The numbers of Heteroptera taken in suction traps during the day and night*

	Trap 3 1950	Trap 3 1953	Trap 3_T 1953	Males Day	Males Night	Females Day	Females Night	Total Day	Total Night
LYGAEIDAE	.	.	.	19	.	9	.	28	.
Peritrechus lundi (Gmelin)	.	1	.	.	.	1	.	1	.
Drymus sylvaticus (Fab.)	.	11	10	15	.	6	.	21	.
Scolopostethus affinis (Schill.)	.	.	1	1	.	.	.	1	.
Taphropeltus contractus (H.-S.)	.	2	3	3	.	2	.	5	.
PIESMIDAE	.	.	.	9	1	8	.	17	1
Piesma maculatum (Costa)	.	9	9	9	1	8	.	17	1
TINGIDAE	.	.	.	1	.	.	.	1	.
Tingis cardui (L.)	.	1	.	1	.	.	.	1	.
NABIDAE	.	.	.	2	.	1	.	3	.
Nabis ferus (L.)	.	2	1	2	.	1	.	3	.
CIMICIDAE	.	.	.	38	3	43	3	81	6
Anthocoris confusus (Reuter)	2	15	21	13	2	22	1	35	3
A. nemoralis (Fab.)	.	1	5	.	.	6	.	6	.
A. gallarum-ulmi (Degeer)	.	.	1	.	.	1	.	1	.
A. nemorum (L.)	2	9	2	7	.	6	.	13	.
Orius majusculus Reuter	.	1	3	2	.	1	1	3	1
O. minutus (L.)	3	7	3	9	1	2	1	11	2
O. niger (Wolff)	.	2	1	2	.	1	.	3	.
Lyctocoris campestris (Fab.)	.	1	3	3	.	1	.	4	.
Xylocoris galactinus (Fieber)	.	1	4	2	.	3	.	5	.
MICROPHYSIDAE	.	.	.	.	1	.	.	.	1
Loricula elegantula (Barensp.)	.	.	1	.	1	.	.	.	1
MIRIDAE	.	.	.	78	31	78	7	156	38
Monalocoris filicis (L.)	2	1	3	1	1	4	.	5	1
Deraeocoris lutescens (Sch.)	1	5	7	7	.	6	.	13	.
Harpocera thoracica (Fall.)	.	2	8	6	.	3	1	9	1
Orthonotus rufifrons (Fall.)	1	.	.	.	1	.	.	.	1
Megalocoleus molliculus (Fall.)	1	.	.	.	.	.	1	.	1
Phylus coryli (L.)	1	.	.	.	.	1	.	1	.
Plesiodema pinetellum (Zett.)	.	.	1	.	.	1	.	1	.
Psallus ambiguus (Fall.)	2	.	.	.	.	2	.	2	.
P. varians (H.-S.)	8	.	7	6	2	7	.	13	2
P. perrisi spp. grp.	25	3	25	22	6	23	2	45	8
P. obscurellus (Fall.)	5	.	.	.	.	5	.	5	.
P. salicellus (H.-S.)	1	.	.	1	.	.	.	1	.
Atractomus magnicornis (Fall.)	1	.	.	.	.	1	.	1	.
Plagiognathus arbustorum (Fab.)	1	.	.	.	.	1	.	1	.
Dicyphus epilobii Reuter	.	.	1	.	.	1	.	1	.
D. errans (Wolff.)	1	1	.	.	.	2	.	2	.
Malacocoris chlorizans (Panz.)	1	.	.	.	1	.	.	.	1
Dryphilocoris flavoquadrimaculatus (Degeer)	1	1	1	2	.	1	.	3	.
Blepharidopterus angulatus (Fall.)	6	1	.	3	2	2	.	5	2
Orthotylus tenellus (Fall.)	1	.	1	.	1	1	.	1	1
O. viridinervis (Kirsch)	1	.	4	2	3	.	.	2	3
O. marginalis Reut.	.	.	1	.	.	1	.	1	.
O. ochrotrichus Fieb.	9	.	.	3	5	.	1	3	6
O. flavosparsus (Sahlb.)	1	.	.	1	.	.	.	1	.
Pseudoloxops coccineus (Mey.-Dür.)	.	1	2	2	1	.	.	2	1
Lygus rugulipennis Popp.	3	1	2	5	.	1	.	6	.
Orthops cervinus (H.-S.)	5	4	10	6	.	12	1	18	1
O. kalmi (L.)	1	.	.	1	.	.	.	1	.
Lygocoris viridis (Fall.)	1	1	1	1	2	.	.	1	2
L. spinolai (Mey.-Dür.)	1	.	.	1	.	.	.	1	.
Calocoris quadripunctatus (Villers)	.	.	1	1	.	.	.	1	.

TABLE IX.—*The numbers of Heteroptera taken in suction traps during the day and night* (Continued)

	Trap 3 1950	Trap 3 1953	Trap 3T 1953	Males Day	Males Night	Females Day	Females Night	Total Day	Total Night
C. norvegicus (Gmelin)	3	.	.	2	.	1	.	3	.
Adelphocoris lineolatus (Goeze)	1	.	.	1	.	.	.	1	.
Stenotus binotatus (Fab.)	2	.	.	1	1	.	.	1	1
Phytocoris tiliae (Fab.)	.	2	2	.	2	1	1	1	3
P. dimidiatus (Kirsch.)	.	1	2	.	3	.	.	.	3
Stenodema calcaratum (Fall.)	1	.	.	.	.	1	.	1	.
S. laevigatum (L.)	.	1	1	2	.	.	.	2	.
Trignotylus ruficornis (Geoff.)	.	1	.	1	.	.	.	1	.
SALDIDAE	.	.	.	2	.	.	.	2	.
Saldula orthochila (Fieb.)	.	1	1	2	.	.	.	2	.
Total—all families: Day	75	87	127	.	.	.	.	.	.
Night	20	3	22	.	.	.	.	.	.
	95	90	149	149	36	139	10	288	46

Trap 4.—A 9-inch Vent-Axia trap was run in a small plot of field beans (*Vicia faba*) in Rothamsted Lodge garden from 8th April to 26th November, 1953. The mouth was 3 feet 6 inches above the ground. This trap is trap 4 of Banks (1959), who gives details of the planting times.

Trap 5.—Another 9-inch Vent-Axia trap was run for the same period in an adjacent plot in Rothamsted Lodge garden. This plot contained a variety of weeds that were known hosts of Heteroptera, including nettles (*Urtica dioica*), mugwort (*Artemisia vulgaris*), fat hen (*Chenopodium album*) and plantain (*Plantago major*). The two traps were about 10 yards apart and some 65 yards from trap 3, which was separated from them by a barrier of ornamental conifers, elm trees (*Ulmus*) and a small lawn. This is trap 5 of Banks (1959).

Trap 6.—A 6-inch Vent-Axia trap was run from 10th June until 6th July, 1953 in the middle of a large patch of nettles (*U. dioica*) in Great Field, 3, Rothamsted Farm. The mouth of the trap was 3 feet above the ground and the nettles 3–4 feet high.

Trap 7.—A 9-inch Vent-Axia trap was operated from 7th May until 31st October, 1954. It was situated in a 13-yard wide headland of rough grass, nettles (*U. dioica*) and other herbage on the SW. side of an oatfield (" Pastures ") on Rothamsted Farm. On the south side of the baulk was a small plantation of conifers, part of Rothamsted Manor wood. There was a small oak (*Quercus*) about 15 yards from the trap.

Cardington Traps

In 1953 Dr. C. G. Johnson and Mr. L. R. Taylor ran four 12-inch Aerofoil traps (enclosed cone type) on a tower on the airfield at Cardington, Bedfordshire, at 9, 21, and 56 (2 traps) feet above the ground. They were run from 22nd September to 28th October and separated the catch into hourly samples. In 1955 these traps were run again with two 30-inch Airscrew traps on barrage balloon cables at 250 and 1000 feet. Heteroptera have been identified from the period 23rd to 31st August.

(2) *Identifications*

The catches from traps 1 and 2 were preserved dry, those from the remainder of the traps in alcohol. All identifications were carried out by the author, generally relatively soon after capture.

(3) *Comparison between Day and Night Catches*

A knowledge of the amount of flight activity of Heteroptera occurring by day and night is not only of intrinsic interest, but also of value in interpreting the data obtained from light traps. The catches from trap 3 were segregated into diurnal and nocturnal; direct comparison is not possible, however, as in 1953 the trap operated for only two hours in the day and for a longer, but varying time at night (*see* p. 186). Even so, the full results (Table IX) show that the Heteroptera, as a group, engage in far more flight activity during the day than during the night. The same picture emerges from the sparser results of the Cardington traps (Table XI), which also indicate that most flight occurs between 12 and 15 hours—the time of maximum temperature.

The Lygaeidae, Piesmidae, Tingidae and Saldidae were all restricted to the diurnal catches; the members of these families were taken mostly during the spring (see p. 202) and are but poorly represented in or absent from light trap catches. Some Cimicidae (about 7 per cent.) were taken at night; this family is also seldom found in light trap catches. Just under 20 per cent. of the Miridae were taken at night and this is the dominant family in light trap catches (Tables XIV and XVII); the most striking feature is, perhaps, that while equal numbers of males and females were taken during the day the males greatly exceeded the females in the nocturnal captures. A few species were caught more frequently at night than during the day; in trap 3 these were: *Orthonotus rufifrons*, *Megalocoleus molliculus*, *Orthotylus viridinervis*, *O. ochrotrichus*, *Malacocoris chlorizans*, *Phytocoris* spp., *Lygocoris viridis* and the microphysid, *Loricula elegantula*. In the Cardington traps *Phytocoris reuteri* was taken just after sunset; it may well be that many of these species are crepuscular rather than nocturnal.

Glick (1939), using traps on aeroplanes, also found far more terrestrial and semi-aquatic Heteroptera by day than by night (1027 : 121); however, he found slightly more corixids at night (53 : 58).

(4) *Comparison between Traps*

(a) *Traps at Different Heights*

In 1953, traps 3 and 3T were in exactly the same situation, but trap 3T was 30 feet above the ground and 25 feet above trap 3. The numbers of individuals and species and their indices of diversity are compared in Table X, from which it will be seen that the upper trap took a greater number of individuals, but the indices of diversity show—not surprisingly—that both traps were sampling the same popula-

TABLE X.—*The numbers of individuals and species of Heteroptera taken in various suction traps run in the grounds of Rothamsted Experimental Station*

(*The index of diversity is calculated from Williams'* (1947) *diagrams.*)

Trap and year	Position	Number of individuals	Number of species	Index of diversity
1, 1947	Garden	21	8	5
2, 1947	Farm	40	13	7
3, 1950	Garden	95	32	16
3, 1953	,,	90	30	16
3_T, 1953	,,	149	35	15·5
4, 1954	,,	118	36	18
5, 1954	,,	253	34	11
6, 1954	Farm	72	9	3
7, 1955	,,	62	22	12
Total all traps		900	85	23

tion. Johnson (1957) has demonstrated that insect density in the air decreases with height; the peculiar result from the upper trap was due in this case to its being in the immediate vicinity of several large trees, especially oak (*Quercus*), whilst the ground flora (a lawn and bedded roses) were not likely to be the habitat of many Heteroptera. A detailed comparison supports this view, the species noticeably more abundant in the upper than in the lower trap being all arboreal (Table IX) namely: *Anthocoris confusus*, *Harpocera thoracica*, *Psallus varians*, *Psallus perrisi* group, *Orthotylus viridinervis* and *Orthops cervinus*, which together account for a difference of 51 individuals. *Anthocoris nemorum* and *Orius minutus* were the only species noticeably more abundant in the lower trap, and these are both herbage dwellers.

A more typical picture of the fall-off of catch with height is given by the Cardington traps (Table XI); allowance must, of course, be made for the larger air intake of the upper traps.

TABLE XI.—*The Heteroptera taken in suction traps at different heights at Cardington, Beds., in* 1953 *and* 1955

(*Note.—The catches are not corrected for the variation in air intake (due to trap size) and running time at the different heights.*)

Species Distribution	1953 22nd Sept.–28th Oct. ♂	♀	T	1955 23rd–31st Aug. ♂	♀	T
Nysius thymi (Wolff)	.	.	.	.	1	1
Scolopostethus thomsoni Reuter	.	.	.	.	1	1
Piesma maculatum (Costa)	.	.	.	8	3	11
Nabis ferus (L.)	.	.	.	.	1	1
Anthocoris confusus Reuter	.	.	.	.	2	2
A. nemoralis (Fab.)	.	.	.	1	.	1
A. nemorum (L.)	.	.	.	3	9	12
Acompocoris pygmaeus (Fall.)	.	.	.	.	3	3
Orius majusculus (Reuter)	.	.	.	4	8	12
O. minutus (L.)	2	2	4	.	1	1
Lyctocoris campestris (Fab.)	1	4	5	2	.	2
Xylocoris galactinus (Fieber)	.	.	.	1	1	2
Orthotylus flavosparsus (Sahlb.)	2	.	2	1	1	2
Lygus rugulipennis Poppius	1	.	1	.	.	.
Orthops cervinus (H.-S.)	.	1	1	.	.	.
O. campestris (L.)	1	1	2	1	1	2
O. kalmi (L.)	5	9	14	.	.	.
Calocoris norvegicus (Gmelin)	.	.	.	.	3	3
Megacoelum infusum (H.-S.)	.	.	.	1	.	1
Phytocoris reuteri Saunders	.	.	.	.	2	2
Trignotylus ruficornis (Geoff.)	.	.	.	.	1	1
	12	17	29	22	38	60
Height Distribution						
9 feet—one 12-inch aerofoil trap	7	6	13	4	12	16
21 feet—one 12-inch aerofoil trap	4	5	9	10	12	22
56 feet—two 12-inch aerofoil traps	1	6	7	7	8	15
250 feet—one 30-inch airscrew trap	Not running			0	5	5
1000 feet—one 30-inch airscrew trap	„		.	1	1	2

Hourly distribution	Heteroptera taken 1953	1955
Hourly period ending		
1 a.m.	1	.
2 a.m.	1	.
3 a.m.	.	.
4 a.m.	.	.
5 a.m.	.	.
6 a.m.	.	.
7 a.m.	.	.
8 a.m.	.	.
9 a.m.	.	1
10 a.m.	1	1
11 a.m.	1	4
12 noon	4	12
1 p.m.	3	10
2 p.m.	4	6
3 p.m.	1	7
4 p.m.	7	2
5 p.m.	2	3
6 p.m.	1	3
7 p.m.	.	.
8 p.m.	.	3
9 p.m.	1	5
10 p.m.	.	3
11 p.m.	.	.
12 midnight	1	.

(b) *Traps in Different Situations*

A comparison between the number of individuals and of species in the main suction traps with their indices of diversity is given in Table X. The most instructive comparison is between traps 4 and 5, which were within 10 yards of one another. The former was surrounded by broad beans, but closer to small fruit trees and a large clump of hedge woundwort (*Stachys sylvatica*) than trap 5, which was surrounded by various weeds that were known hosts of Heteroptera (*see* p. 188). Trap 5 took over twice as many individuals as trap 4; this larger catch was partly because certain species whose hosts were on the plot were more abundant in trap 5. These were *Orthotylus ochrotrichus* (5 more), *O. flavosparsus* (40), *Lygocoris lucorum* (14); other species were confined to trap 5, namely *Orius niger* (3) and *Plagiognathus albipennis* (9), host plant mugwort (*Artemisia vulgaris*), and, most spectacular, *P. arbustorum* (28), whose immediate host plant was nettles. Together these six species accounted for an extra 99 individuals in trap 5. The greater diversity of trap 4 was due to the presence in low numbers of four apple and two *Stachys* species, which were absent from trap 5. The predatory *Anthocoris nemorum* was present in both plots, but slightly larger numbers were taken in trap 5; another predator, *Deraeocoris ruber*, was also more abundant in trap 5. Lygaeids, *Piesma* and *Tingis*, were taken in almost equal numbers in the two traps; the same applied to these groups in traps 3 and 3T. Trap 6 was in a nettle patch near an oak tree and every species taken was attached to one of these two plants; the catch was, however, dominated by the nettle lygaeid, *Heterogaster urticae* (56 individuals).

In conclusion, suction traps, like light traps, show that much of their catch is drawn from their immediate surroundings. Although some species, such as *Piesma maculatum*, occur in most traps, even away from their hosts, and others, such as *Anthocoris nemorum*, are ubiquitous both in trap catches and in nature, the catches of the majority of species are much influenced by the proximity or otherwise of their host plants to the trap. This was strikingly demonstrated in the case of *Plagiognathus arbustorum*, a very common mirid of nettles (*Urtica dioica*) and other rank herbage, of which 28 specimens were taken in trap 5 and none in trap 4 only 10 yards away.

III. General Comparisons

(1) *Comparison of Light and Suction Trap Data*

A detailed comparison of the catches by light and suction traps can be made from Table XVII; certain salient features, however, call for comment.

(a) *Families*

The light trap catches are completely dominated by the Miridae which make up 97 per cent. of the total catch, whereas in the presumably unbiased sample of the flying population taken by suction traps they form 56 per cent. of the total. The lygaeoid families (Lygaeidae, Piesmidae and Berytidae) and the Cimicidae are only represented in the light trap catches to the extent of 0·002 per cent. of the total, whilst in suction trap samples they made up 18 per cent. and 24 per cent. respectively of the total catch.

These differences are to some extent accounted for by the largely diurnal flight habits—in temperate countries—of the lygaeids and cimicids, already discussed (p. 188, Table IX), 82 per cent. of the night catch of suction traps being mirids. There is, however, a much lower proportion of cimicids in the light traps than in the night catches of the suction trap. It seems probable that these families also differ in their reaction to light.

(b) *Differences in Species*

The five most abundant mirids in the suction traps were *Orthotylus flavosparsus* (91), *Plagiognathus arbustorum* (40), *Calocoris norvegicus* (33), *Lygus rugulipennis* (28) and *Orthops cervinus* (28); the corresponding species for the light traps are given in Table II and are *L. rugulipennis* (1406), *Adelphocoris lineolatus* (583), *Megalocoleus molliculus* (411), *Orthotylus flavosparsus* (378) and *Orthops kalmi* (238). It is realised that the majority of the light trap records come from traps situated somewhere on the farm, whilst most of the suction traps were in Rothamsted Lodge garden, but light trap D was in the Lodge garden and for the two years (1948 and 1949) in which it was operated the five most abundant species were *L. rugulipennis* (255), *A. lineolatus* (83), *M. molliculus* (67), *O. flavosparsus* (26) and *Orthops cervinus* (25).

In addition a direct comparison is possible for July to September, 1947 between suction trap 2 and light trap C, which were within 20 yards of one another in a uniform habitat. The five species most abundant in the light trap were *Lygus rugulipennis* (240), *Orthotylus flavosparsus* (131), *Adelphocoris lineolatus* (109), *Megalocoleus molliculus* (50) and *Orthops kalmi* (44). The suction trap catches were unfortunately few in number, but *L. rugulipennis* and *O. flavosparsus* were the two most abundant species (12 individuals each); the third mirid was *Calocoris norvegicus* (5). One specimen was taken of *O. kalmi*, whilst *A. lineolatus* and *M. molliculus* were unrepresented in the suction trap catches.

There is thus a striking parallel between the general comparison and particular cases, *L. rugulipennis* and *O. flavosparsus* are well represented in both types of traps, *Orthops kalmi* and *O. cervinus* moderately so (*see also* Table XVII), but *A. lineolatus* and *M. molliculus* are hardly represented at all in suction trap catches (one specimen of each). In contrast, *Calocoris norvegicus* is seldom taken in light traps (11 individuals in eight trap years) and *Plagiognathus arbustorum* even less often (only one specimen). In Rothamsted Manor wood, the host plants, especially nettles (*Urtica dioica*), of these two last-named mirids were abundant, yet in the intensive light trapping experiment in this wood *C. norvegicus* and *P. arbustorum* were still taken in low numbers (*see also* p. 206, 208 and Table V).

Thus light traps, sampling as they do only the small crepuscular and nocturnal parts of the population of flying Heteroptera, fail in temperate, but not in tropical (Table XIV) countries, to sample certain families in any numbers, and hence the generally lower indices of diversity of light traps compared with suction traps (*cf.* Tables III and X). Light traps do, however, catch large numbers, much larger than are taken by suction traps (incidentally none were taken in the suction trap at Tafo, Table XIV). Sometimes species abundant in light trap catches are also abundant in the flying population (e.g. *Lygus rugulipennis*), but in other cases light trap catches greatly exaggerate (e.g. *Adelphocoris lineolatus*) or greatly underestimate (e.g. *Calocoris norvegicus*) the flying population of a species. Several other examples can be seen in Table XVII. Whether these false estimates are due to differing times of flight or variation in the reaction to light cannot be stated on the present evidence; suggestions, with evidence, in individual cases are given in section IV(1).

(2) *The Flight Activity of the Two Sexes*

Thomas (1938) noted the preponderance of males in light trap catches of Miridae; the same picture has emerged in the present work (Table XVII, 84 per cent. males), and it has already been shown that the excess of males is increased in ultra-violet trap catches (p. 183). The limited data from suction trap 3, the only one segregating day and night catches (Table IX), suggest that at night males (82 per cent.) predominate over females in the flying population of mirids, although during the day the numbers are almost equal. The figures for all suction traps (Table XVII), most of which were running continuously, show that males make up 73 per cent. of the total

catch. In view of the fact that only 20 per cent. of the total mirids are taken at night (p. 189), the proportion of males in these catches is too high to support the hypothesis of equal numbers during the day.

Although the general picture in the Miridae therefore shows more flight in males than in females, there are a certain number of exceptions. In *Deraeocoris lutescens*, *Orthops cervinus* and *Calocoris norvegicus* females exceed males in the suction trap catches (Table XVII). In the light traps 74 per cent. of the catch of *O. cervinus* were males—a figure somewhat less than the family average ; much smaller numbers of the two other species were taken in the light traps, but in both cases females predominated.

In the present series of light trap catches female Cimicidae predominate over males. Thomas (1938), however, found almost equal numbers. The much larger sample taken by the Rothamsted suction traps showed that males exceed females by almost two to one, whilst in the higher level traps at Cardington the reverse applied (Table XI).

As Thomas (1938) found, equal numbers of both sexes of Nabidae are caught by light and suction traps ; the same applies to suction trap catches of Piesmidae. Even when allowance is made for the swamping effects of *Heterogaster urticae*, males slightly exceed females in the suction trap catches of Lygaeidae.

The only pentatomid taken in any numbers was *Pentatoma rufipes* in the Rothamsted light traps (Tables V and XVII). Here males exceeded females, but the females just predominated in the Kawanda and Tafo light traps (Southwood, 1960).

(3) *The Flight Activity, its Frequency and Duration*

(a) *Frequency*

It is obvious that short-winged Heteroptera, such as the females of *Loricula elegantula* and *Mecomma ambulans* and most adults of *Dolichonabis limbatus*, cannot fly. The work of Jackson (1933, 1952 and 1956) with *Sitona* and water beetles, and that of B. Johnson (1953, 1957) with aphids has shown that some apparently fully winged insects are incapable of flight because their wing muscles are absent or reduced. Poisson (1924) has made similar observations on certain aquatic Heteroptera : *Ilyocoris cimicoides* (L.), for example, completely lacks flight muscles although the hind wings are large and membraneous.

There is little concrete evidence as to whether some terrestrial Heteroptera engage in more flight activity than others, either from behavioural or morphological causes. Thomas (1938) drew attention to the apparent discrepancies between light trap numbers and " commonness " in the field, and Johnson and Southwood (1949) maintained, on the basis of balloon net catches, that *Lygus rugulipennis* must engage in more flight activity of a type that would lead to its presence in the upper air than do most other Heteroptera.

Some information on the comparative flight activity of different species of Heteroptera can be obtained from observations made by the author in 1954 on Rothamsted Farm. A 9-inch Vent-Axia suction trap (7) was run continuously in a headland at the edge of a field and alongside a small conifer plantation. A small cavity was dug under the trap and it was so arranged that its mouth was only 2 feet 4 inches above the surface of the ground—about level with the mean height of the vegetation. About half the headland was covered with mixed herbage, mostly nettles (*Urtica dioica*) and creeping thistle (*Cirsium arvense*) ; the remaining half was rough grass, chiefly *Holcus* and *Dactylis*. The headland was swept every week from May until October for the main part of the Heteroptera season (30th June to 8th October) ; this was standardised at 20 yards of grass and 15 yards of nettles and other herbage.

From 1st June until late September ten samples (each of about 0·8 sq. ft.) were taken from herbage each week with a suction (or vacuum) apparatus, which gives

TABLE XII.—*A comparison of the numbers of adult Heteroptera in an area (from suction apparatus and sweeping samples) and the numbers taken in the suction trap*

(+ *Grass-dwelling species.* * *Species entirely confined to various trees occurring in the neighbourhood and therefore unlikely to be found in the suction apparatus or sweeping samples.*)

	Suction apparatus			Sweeping			Suction trap		
	♂	♀	T	♂	♀	T	♂	♀	T
ARADIDAE									
Aradus depressus (Fab.)*	.	.	.	.	.	.	1	1	2
PENTATOMIDAE									
Eysarcoris fabricii Kirk.	.	.	.	5	.	5	.	.	.
LYGAEIDAE									
Heterogaster urticae (Fab.)	.	.	.	1	.	1	.	.	.
Drymus sylvaticus (Fab.)	.	1	1	.	.	.	.	.	.
Scolopostethus affinis (Sch.)	.	.	.	4	13	17	.	.	.
PIESMIDAE									
Piesma maculatum (Costa)	.	.	.	.	.	.	1	.	1
TINGIDAE									
Tingis ampliata (H.-S.)	.	1	1	.	.	.	.	.	.
T. cardui (L.)	.	.	.	.	.	.	.	1	1
NABIDAE									
Nabis ferus (L.)	.	1	1	.	1	1	.	.	.
N. rugosus (L.)	.	1	1	1	4	5	.	.	.
Stalia major (Costa) +	.	.	.	1	1	2	.	.	.
Dolichonabis limbatus (Dahl.) +	29	21	50	26	32	58	.	1	1
CIMICIDAE									
Anthocoris confusus Reut.	.	.	.	2	3	5	.	.	.
A. nemorum (L.)	1	3	4	105	122	227	4	3	7
Acompocoris pygmaeus (Fall.)*	.	.	.	.	.	.	1	.	1
Orius majusculus Reut.	.	.	.	2	1	3	.	.	.
MICROPHYSIDAE									
Loricula elegantula (Barensp.)*	.	.	.	.	.	.	1	.	1
MIRIDAE									
Deraeocoris lutescens (Sch.)	.	.	.	3	1	4	.	.	.
D. ruber (L.)	.	.	.	.	.	.	2	.	2
Harpocera thoracica (Fall.)*	.	.	.	.	.	.	1	1	2
Tythus pygmaeus (Zett.)	1	.	1	.	.	.	.	.	.
Orthonotus rufifrons (Fall.)	.	.	.	1	.	1	.	.	.
Psallus perrisi Wagn.*	.	.	.	.	.	.	.	1	1
P. falleni Reut.	.	.	.	.	1	1	.	.	.
Atractotomus magnicornis (Fall.)*	.	.	.	.	.	.	3	1	4
Plagiognathus arbustorum (Fab.)	.	1	1	50	65	115	9	1	10
P. chrysanthemi (Wolff)	.	.	.	1	4	5	.	.	.
Dicyphus stachydis Reuter	.	.	.	.	1	1	.	.	.
Mecomma ambulans (Fall.) +	1	16	17	4	3	7	2	.	2
Pithanus maerkeli (H.-S.) +	.	2	2	.	.	.	.	.	.
Lygus rugulipennis Popp.	.	.	.	1	1	2	1	.	1
Liocoris tripustulatus (Fab.)	.	.	.	12	16	28	.	.	.
Lygocoris pabulinus (L.)	.	.	.	2	1	3	.	.	.
L. lucorum (Mey.-Dür.)	.	.	.	1	2	3	1	2	3
Orthops rubricatus (Fall.)*	.	.	.	.	.	.	3	.	3
O. kalmi (L.)	.	.	.	1	.	1	4	1	5
Calocoris sexguttatus (Fab.)	.	.	.	2	1	3	.	.	.
C. norvegicus (Gmelin)	.	.	.	5	6	11	3	3	6
Stenotus binotatus (Fab.)	.	1	1	15	22	37	1	1	2
Capsus ater (L.)	13	19	32	2	3	5	.	.	.
Stenodema calcaratum (Fall.) +	2	2	4	9	11	20	2	.	2
S. laevigatum (L.) +	.	6	6	11	50	61	.	1	1
Notostira elongata (Geoff.) +	.	.	.	1	1	2	.	.	.
Leptopterna dolabrata (L.) +	2	1	3	17	13	20	2	4	6

extraction rates that are usually above 95 per cent. of the population (Johnson, Southwood and Entwistle, 1957). Unfortunately the samples were not primarily taken for the purposes of the present comparison and only the grasses were sampled with the suction apparatus.

The results are given in Table XII. If the grass dwellers (marked +) are considered it will be seen that, apart from the short winged *Dolichonabis limbatus*, the mirid *Capsus ater* was the most numerous species. The wings in this species are fully developed and yet it is obviously very inactive, for not only was it never taken in the suction trap, but it was also comparatively rare in sweeps, generally remaining around the roots of grasses. The Stenodemini and *Stenotus binotatus* were present in smaller numbers, but because of their habit of frequenting the tops of grasses larger numbers than of *C. ater* were taken by sweeping. *Stenodema laevigatum* appeared to show rather less flight activity than *S. calcaratum* ; the figures in this case are rather small but the conclusion is also supported by the total light and suction trap catches (Table XVII). *Pithanus maerkeli* is micropterous, as is the female of *Mecomma ambulans*. For their low population[1] the males of *M. ambulans* appear to have a high level of flight activity. This is in accordance with field observation : they frequently take flight in the sweep net and their markings and movements are such that they may momentarily be confused with a small ichneumonid.

With the nettle and other herbage species (unmarked), comparison must be made between the figures for sweeping and the suction trap. *Anthocoris nemorum* and *Plagiognathus arbustorum* were both dominant in sweepings and trap catches. The trap was very close to the nettles and so this record is by no means contrary to the findings with traps 4 and 5 (p. 191). These two species obviously engage in considerable flight activity (albeit of short range in *P. arbustorum*). Of the less abundant species the fully winged *Liocoris tripustulatus* was not taken in the suction trap ; there is also further evidence (p. 208) to show that this mirid has, in England at least, a very low level of flight activity. In contrast, fewer specimens of *Calocoris norvegicus*, *Lygus rugulipennis* and *Orthops kalmi* were taken and all were represented in the trap catch, which indicates that the large flying population of these species, already noted (p. 192), is *not* just a reflection of abundance in the field.

The presence of *Piesma maculatum* and *Tingis cardui* in the suction trap catches is worthy of mention, as the food plant of neither species was present in the headland, and it has been suggested earlier (p. 191) that the catches of these species are less influenced by the immediate surroundings of the trap than is the case with many mirids. The predatory *Deraeocoris ruber* was also not recorded in the adult state in the sweeps ; larvae were, however, taken, so that the species was definitely breeding in the headland.

The different sized populations of various species of flying Heteroptera alluded to on p. 192 may therefore, in fact, be due to differing frequencies and intensities of flight as well as to different sized absolute populations.

(b) *Duration*

The duration of flight and its range are to some extent different aspects of the same phenomenon. An insect that flies for a long period at a time is more likely, other things being equal, to travel further from its original habitat than one that flies for only a short while. An insect flying voluntarily for a short distance may, of course, under certain circumstances, be carried much further by air currents, and in addition, the duration of flight in any individual will depend on its physiological condition.

[1] It must be noted that this is a cumulative population, the males, being much shorter lived than the females, have a much lower cumulative population, although the absolute numbers may have been similar.

The comparisons between traps of the same type (sections I (4) p. 179 and II (4) p. 189) have in both cases shown that the catches are very considerably affected by their immediate environments—their differing indices of diversity are a result of this. If the Heteroptera taken in traps are so dependent on the surroundings, then their flight range must be small and short flights in the immediate proximity of the host would be their commonest behaviour. The mirid *Plagiognathus arbustorum* (pp. 191, 195) and the lygaeid *Heterogaster urticae* (p. 191) are perhaps extreme examples of this type of behaviour. There were certain exceptions to the general conclusions that the catches of Heteroptera were especially dependent on the immediate environment of the traps. The host plants of *Piesma maculatum* are various wild and cultivated Chenopodiaceae ; none of these grew near suction traps 3 or 7 and yet these traps, like all others running in the spring (Table XV), took some numbers of this species. *Tingis cardui*, *Taphropeltus contractus* and *Adelphocoris lineolatus* are other bugs that show this wide range of flight—in the case of the last named only detected by light traps (p. 209).

The lygaeoids[2] and *T. cardui* are taken mostly in the spring, and this wide ranging flight is therefore really a post-hibernation flight of the type observed on a small scale by Tischler (1937) and others in pentatomids, and carried to the extreme in Heteroptera by the migrating shield bug *Eurygaster integriceps* (Fedotov, 1947–55).

Some simple laboratory experiments were carried out to test the duration of flight in various Heteroptera. The specimen was held suspended from a blunt pin attached to the dorsum of the thorax by adhesive ; quick drying cellulose paint was found very suitable for this purpose. The insect lifted sharply from the substrate and moved forwards through the air ; as the tarsi lost contact the wings were opened and in many cases flight commenced. Because the bugs were not supporting their own weight, the figures obtained are maximal.

The majority of the experiments were made on 5th and 20th May in a laboratory where the temperature was between 66 and 68° F. (19 and 20° C.). Some species, once started, would continue flying for a lengthy period. These were :

Sehirus bicolor : males and females flew for an average of 57 minutes (shortest period 6 minutes, longest 170 minutes).

Piesma maculata : males and females flew for 32 minutes (shortest 15 minutes, longest 75 minutes).

Berytinus minor : male flew for 42 minutes.

Other species would fly only for a minute or so, requiring frequent restarting ; these were *Stenodema laevigatum* females (maximum period 10 minutes, mean 3 minutes) ; *Harpocera thoracica* unmated males and females (maximum period 3 minutes, mean less than 1 minute) ; and *Stenotus binotatus* males (mean half a minute ; experiment made on 16th July). It may be that the failure to maintain prolonged flight in the mirids was due to faulty experimental technique, *e.g.* not flying them in a continuous air stream. It is, however, conclusive that in the spring certain overwintered pentatomoids and lygaeoids are capable of sustained flights of some duration. Flight was successfully initiated only in one female of *Sehirus bicolor* ; by early May most females would be " brooding " their egg masses (Southwood and Hine, 1950). Females removed from their egg masses could not be induced to fly.

Field observations were carried out on 25th, 26th and 27th May on the flight distances of females of *Stenodema laevigatum* amongst rough grass on Rothamsted Farm. The results are given in Table XIII. It will be seen that most of the flights were of a few inches ; they were seldom more than a foot above the general level of the vegetation, but the sixth individual finally rose to 15 feet above the ground and was lost to view. Detailed observations at the time also suggested that the higher the level of flight above the top of the vegetation the greater the flight distance.

[2] " Lygaeoids " is used here to cover Lygaeidae, Berytinidae and Piesmidae.

TABLE XIII.—*Flight distance of six female* Stenodema laevigatum (*L.*) *measured in the field on 25th–27th May*, 1954

Number of flights	Flight distance		Mean (inches)	S.D. of mean
	Longest	Shortest		
28	127	1	18·7	28·1
7	264	5	81·8	90·1
5	117	5	33·6	48·2
13	117	4	28·5	31·8
20	43	1	17·3	15·6
14	156	2	17·5	40·1

S. laevigatum always took off from the tops of grass blades and the hind legs were moved forward prior to take-off, so that the initial launching was probably a combination of a jump and flight and its success may have determined the length of the flight.

The laboratory experiment demonstrates that some Heteroptera are capable of flight of such a duration that the range of a single flight could be some miles. Others may fly for shorter times and distances, " flits ", but a series of these short flights may, under certain conditions (perhaps a good take-off) be followed by one of at least several yards and then the insect could be carried by air currents to considerable heights and distances.

Considered against the background of the previous conclusions, it seems that the post-hibernation flight of many lygaeids (e.g. *Drymus*, *Taphropeltus*), *Piesma*, *Tingis* and some pentatomoids (e.g. *Sehirus*) is of long duration and leads to dispersal. In those species that do not hibernate as adults, e.g. *Pentatoma rufipes*, *Plagiognathus arbustorum*, the majority of the flights are of short duration, *i.e.* flits. Males engage in flits more than females, and a high proportion of males in a suction trap catch close to the host plant would indicate a population with this type of flight. However, some individuals from such populations must engage in longer flights that will lead to dispersal.

All the Heteroptera taken in the higher Cardington traps (Table XI) must be considered as engaging in dispersive movement, and even in the non-hibernating species the sex ratio differed from that in the lower traps at Rothamsted, females predominating over males. Therefore the hypothesis that all dispersal in these bugs is due to flits being prolonged into longer flights by air currents is not tenable (if it were males would predominate at all heights). Some dispersive flight may be due to this ; but some, especially in the female, must also be due to flight differing in its characteristics from a flit.

(4) *Comparison of the Constitution of Trap Catches at Harpenden, England, with Those Made Elsewhere*

The value of any general conclusions drawn from Harpenden data (Thomas, 1938, and Tables II and XVII) would be considerably enhanced if it could be shown that a similar pattern of families and major species has been obtained in other parts of Britain and the world.

(a) *Previous Work—Sites and Traps*

1. *Johnson and Southwood* (1949) record the Heteroptera taken in tow-nets flown at 50–3000 feet from 23rd June to 31st October, 1947 and from May to October, 1948 over an airfield at Cardington, Beds. The site has been described in more detail by Giblett *et al.* (1932) and Johnson (1957).

2. *Southwood and Johnson* (1957) ran an 18-inch propeller-type suction trap in the middle of a field of winter wheat at Ardington, Berks., from 8th to 12th May,

1954. The field was part of a large farm intersected by many ditches and large hedges ; the latter contained numerous good-sized oak trees.

3. *Freeman* (1939) trapped at Tetney, Lincs., at 10, 177 and 277 feet above the ground with tow-nets in September and October, 1934 and from March to November, 1935. The land around the trapping site was very flat, mainly reclaimed from the sea, with numerous dykes ; the sea wall and a salt marsh were about two miles to the east.

4. *Hardy and Milne* (1938) trapped with tow-nets at various heights ; the only heteropteran taken was at 450–600 feet near Dover.

5. *Glick* (1939) collected insects in traps on aeroplanes flying at heights of 20–11,000 feet in Louisiana, U.S.A., over a rich subtropical forest and swamp region, with comparatively small areas of cultivation.

6. *Glick* (1939) made similar collections by aeroplane over an artificially irrigated area surrounded by barren deserts and mountains in Mexico.

7. *Glick* (1957) made further " aeroplane collections " at 100–5000 feet over the restricted irrigated areas of the Rio Grande Valley, Texas, U.S.A., which are surrounded by semi-arid mesquite chaparral.

8. *Frost* (1952) records the more abundant Miridae taken in 18 light traps operated 6–8 feet above the ground, in various localities in Pennsylvania, U.S.A. ; they were mainly operated from 15th May to 20th September.

9. *Cumber* (1950) operated a modified Rothamsted light trap on the edge of a *Phormium* plantation by the Manawatu River at Paiaka, New Zealand, from July, 1949 to July, 1950 ; details of the Heteroptera taken are given in Cumber (1953).

10. *Meurer* (1956, 1957) ran a Robinson-type light trap at Heemstede, near Haarlem, Holland, from 2nd May to 1st November, 1954 and from 5th April to 1st October, with four odd nights in October and November, 1955. This trap was situated in an orchard surrounded by deciduous trees—oak (*Quercus*), hawthorn (*Crataegus*), birch (*Betula*), hazel (*Corylus*), willow (*Salix*), sloe (*Prunus*) and juniper (*Juniperus*).

(b) *Additional New Data—Sites and Traps*

1. *Kawanda, Uganda.*—Mr. T. R. Odhiambo kindly collected the Heteroptera during the new moon periods 6th to 12th January and 8th to 11th February, 1959 from the Robinson-type mercury vapour light run at Kawanda Research Station. The trap is in a coffee plantation where large *Albizzia stipulata* trees provide the canopy ; the nearest fresh water is a swamp three-quarters of a mile away. The trap was run from 6.30 p.m. to 7.45 a.m. Mr. Odhiambo (*in litt.*) commented on my analysis of the catches (Table XIV) as follows: " They in general conform to the sort of proportional numbers one expects at Kawanda ... Three families are not represented in the January and February ' new moon ' periods' catches : Anthocoridae [= Cimicidae], Corixidae and Notonectidae ; they come in one's and two's and their absence in the catches is not therefore surprising ".

2. *Tafo, Ghana.*—Dr. M. R. Smith was kind enough to run a simple light trap with a UV bulb over a metal funnel, 3 feet above the ground in a cocoa plantation under forest canopy at the West African Cocoa Research Institute. This trap and a 9-inch Vent-Axia suction trap, in the same situation, were run from 24th March to 20th April, 1959. Although the suction trap ran during the day and night it did not take a single heteropteran.

(c) *Discussion of Results*

The numbers of the different families are given in Table XIV, and it can be seen that there is considerable similarity. Of the terrestrial families the Miridae, the Lygaeidae and the Cimicidae are usually the most numerous in this order in temperate

TABLE XIV.—*The numbers of individuals of the different families of Heteroptera taken in traps in various parts of the world*

	Author	Thomas (1938)				Johnson and Southwood (1949)	Southwood and Johnson (1957)	Freeman (1939)	Glick (1939)	Glick (1939)	Glick (1957)	Cumber (1950)	Meurer (1956, 1957)		
	Place	Harpenden, England	Harpenden, England	Harpenden, England	Cardington, England	Cardington, England	Ardington, England	Tetney, England	Louisiana, U.S.A.	Mexico	Texas, U.S.A.	Paiaka, New Zealand	Heemstede, Holland	Kawanda, Uganda	Tafo, Ghana
	Type of trap	Light	Light	Suction	Suction	Tow-nets	Suction	Tow-nets	Aeroplane	Aeroplane	Aeroplane	Light	Light	Light	Light
FAMILY															
Aradidae				2					4						
Acanthosomidae		4	1									1	7		
Cydnidae			1				1		66	2	1			154	993
Scutellaridae															7
Pentatomidae		18							10	1			4	12	51
Coreidae									2					1	1
Alydidae														65	24
Rhopalidae									22	1				1	
Pyrrhocoridae														1	2835
Largidae															177
Lygaeidae		11	3	110	2	1	4	18	341	22	22	1	1	801	559
Piesmidae			1	39	11	2	99	52	1	1					
Berytinidae				1			15		30	1					
Reduviidae		1							2		4			26	17
Tingidae				5					44		7			4	
Nabidae		90	17	6	1			2	7		4			7	75
Cimicidae		14	7	206	44	10	17	8	221		6		9		
Microphysidae		1		2											
Isometopidae														1	
Miridae		5741	1385	527	31	27	5	7	156	48	35	200	1542	226	38
Saldidae				2			1		5				3		
Enicocephalidae									22					3	3
Mesoveliidae									1		1			1	
Hebridae									8						
Hydrometridae									1					1	
Veliidae									2						
Gerridae									1					2	
Belostomatidae														1	
Corixidae		12	42						111				910		

regions, the Lygaeidae dominating in the tropics. The most abundant species are given in Table XV; again certain similarities are striking, more especially in view of the geographical diversity of the trap locations. Meurer's (1956, 1957) trap was in semi-woodland conditions that showed a greater resemblance to those of trap E_1 than to any other in the present work; it is not surprising, therefore, that his catch was dominated by certain woodland species. These, which were not included in Table XV, were *Blepharidopterus angulatus* (93 specimens), *Lygocoris pabulinus* (92), *Orthotylus marginalis* (39), *O. diaphanus* (37) and *Harpocera thoracica* (taken in large numbers on a few nights, p. 206). A feature of great interest in Meurer's (1956) paper is a list of species common in the area but not taken in his trap. The list includes *Monalocoris filicis*, *Plagiognathus arbustorum*, *Heterotoma merioptera*, *Calocoris norvegicus*,

TABLE XV.—*Comparison of the more abundant species in the major trapping records from temperate and subtropical countries*

(*Figures in italics are catches of the particular species when it was not amongst the more abundant species; the more abundant species were taken as the five with the largest catches when the total catch was over* 1000, *the four largest when the total catch was between* 100 *and* 1000, *and the three largest when the total catch was under* 100.

	Place	Harpenden, England	Harpenden, England	Cardington, England	Ardington, England	Tetney, England	Louisiana, U.S.A.	Mexico	Pennsylvania, U.S.A.	Heemstede, Holland		
	Author			Johnson and Southwood (1949) and Table XI	Southwood and Johnson (1957)	Freeman (1939)	Glick (1939)	Glick (1939)	Frost (1952)	Meurer (1956, 1957)		
	Type of trap	Light	*Suction	Tow-nets	Suction	Tow-nets	Aeroplane	Aeroplane	Light	Light (non-woodland species)	Species shown to have a high level of flight activity (p. 194, Table XII)	Species with temporary habitats
MIRIDAE												
Lygus spp.		1771	*28*	23	*4*	.	55	.	2233	71	+	++
Adelphocoris spp.		762	*1*	.	.	.	.	12	2134	*8*	+	+++
Orthops kalmi (L.) and *O. basalis* Costa		256	*28*	17	.	.	.	.	.	28	+	++
Trignotylus spp.		*65*	*1*	*1*	.	.	.	11	3472	*10*	.	.
Orthotylus flavosparsus (Sahlb.)		256	91	*4*	.	.	.	.	809	31	.	+
Megalocoleus molliculus (Fall.)		328	*1*	.	.	.	.	.	.	*10*	.	++
Plagiognathus politus Uhler		.	.	.	.	.	.	.	3368	.	.	++
Calocoris norvegicus (Gmelin)		*11*	33	*3*	.	*1*	.	.	.	.	+	+
Plagiognathus arbustorum (Fab.)		*1*	40	.	.	.	.	.	.	.	.	.
LYGAEOIDEA												
Antillocoris spp.		.	.	.	.	.	51	.	.	.	.	+
Drymus sylvaticus (Fab.)		.	*27*	*1*	.	11	.	.	.	.	.	.
Nysius spp.		*1*	.	*1*	.	.	53	17	.	.	.	++
Piesma spp.		.	*39*	13	99	52	*1*	*1*	.	.	+	++
Cymus spp.		.	.	.	15	4	.	.	.	.	.	+
TINGIDAE												
Tingis cardui (L.)		.	*4*	.	7	.	.	.	.	.	+	+
CIMICIDAE												
Orius spp.		*1*	*29*	*9*	.	*3*	221	.	.	*3*	.	+
Anthocoris nemorum (L.)		*6*	110	16	.	.	.	.	.	*6*	.	.
Lyctocoris campestris (Fab.)		*4*	6	*7*	10	*1*	.	.	.	.	.	+
Xylocoris galactinus (Fieber)		.	*7*	*4*	*3*	*2*	.	.	.	.	.	+
CYDNIDAE												
Amnestus pusillus Uhler		.	.	.	.	.	42	.	.	.	.	+

* Heterogaster urticae *taken in only one trap* (*p.* 191) *is omitted.*)

Orthops campestris and *Liocoris tripustulatus*. All these mirids were abundant at Rothamsted and there, too, they were absent or poorly represented in the light trap catches (Table XVII).

The light trap catches from tropical regions—Kawanda (Kenya) and Tafo (Ghana)—differ from the catches made elsewhere mostly in the dominance of lygaeoid families over the Miridae. As the nearby suction trap at Tafo failed to catch any

Heteroptera, it is not known whether this represents the true picture of the comparative amounts of flight in the different families, but it does seem to indicate that the light trap exaggerates considerably the amount of flight in the area. The Kawanda trap catches contained a large number of species, but those at Tafo were dominated by the pyrrhocorid, *Dysdercus melanoderes* Karsch, which made up 59 per cent. of the total catch over the whole period, and on some nights almost the entire catch : *e.g.* on 29th March, out of a catch of 58, all but one specimen belonged to this species. These pyrrhocorids and the Largidae (details are given in Southwood (1960)) are probably associated with the shade trees. Nearly half the Miridae were taken on 8th April and, although about 14 different species were taken, they did not include the cocoa mirids, *Sahlbergella* and *Distantiella*. It seems probable, therefore, that the Tafo catches, because of the rather special and uniform environment of the trap (*i.e.* cocoa and litter, with the shade trees considerably above), are atypical. The uniformity of the environment is reflected in the large numbers of individuals of a small number of species of Pyrrhocoridae, Largidae (all but one were *Physopelta analis* Sign.), Lygaeidae, Alydidae (all *Leptocorisa apicalis* Westwood) and Cydnidae.

IV. Conclusions

(1) *Systematic Consideration of Flight Activity*

The present study, more especially when considered in conjuction with previous work (p. 197, Tables XIV and XV), enables definite characteristics to be given for the flight activity of various taxa—principally certain families and common species.

Aradidae

Lindsey and Usinger (1944) and Glick (1939) record flights of various aradids, and that of *Aradus depressus* is recorded here. There is some evidence that these flights coincide with those of subcortical and wood boring beetles (Southwood and Johnson, 1957). Stichel (1936) also observed flight in two species of *Aradus*.

Cydnidae

Thomas (1938) recorded *Sehirus bicolor* from the Rothamsted light trap and Southwood and Johnson (1957) from suction trap catches at Ardington and it has been shown (p. 196) that this species may fly for as long as three hours, in which time it could theoretically cover about 25 miles. Glick (1939) records 76 cydnids in Louisiana. Leston (1957) remarks how two species, *Aethus indicus* and *Geotomus pygmaeus*, are known to spread rapidly. There are also numerous records of cydnids, sometimes in large numbers, at light (Wolcott, 1948 ; Callan, 1954) and very large numbers were taken at Kawanda and Tafo (Table XIV). The Cydnidae, a smaller family than the Pentatomidae, therefore show a higher level of flight activity. In England this is mostly in late spring, being post-hibernation flight.

Scutellaridae

The only evidence from the present work is 7 specimens taken at Tafo ; the pre- and post-hibernation flights of *Eurygaster integriceps* in Russia, Persia and Asia Minor are, however, well known (Fedotov, 1947–55 ; Vodjdani, 1954).

Pentatomidae

Pentatoma rufipes is the only member of the Pentatomidae (*sensu stricto*) taken in light traps at Harpenden (Table XVII), in Holland (Meurer, 1956, 1957) and at house lights in Berlin (Stichel,1936). This is also the only shield bug in this region that overwinters as a larva and is therefore present in the field as an adult during the

period of highest temperature, *i.e.* July and August. Glick (1939) took only ten pentatomids in his aerial collections over Louisiana, and small numbers were obtained at Kawanda and Tafo (Table XIV). Thus, in spite of Le Quesne's (1946) report of a mass flight of *Piezodorus lituratus* (Fab.) in Jersey, available evidence suggests that Pentatomidae engage in less flight activity than some other families of shield bugs—Cydnidae and possibly Acanthosomidae.

Acanthosomidae

Although there are only three common European species, all have been taken at lights as follows: *Acanthosoma haemorrhoidale* (Stichel, 1936; Thomas, 1938; Meurer, 1957; and the present author), *Elasmostethus interstinctus* (Stichel, 1936; Meurer, 1956, 1957; and the present author) and *Elasmucha grisea* (Stichel, 1936). The only shield bug taken in New Zealand in Cumber's (1953) light trap was the acanthosomid, *Oncacontias vittatus* (Fabr.). The reason for these catches may be because acanthosomids show more flight activity than pentatomids or because they possess nocturnal flight habits and positive reaction to light.

Coreidae sensu lat.

This family is divided by many workers into three separate families, the Coreidae (with most species), the Alydidae and the Rhopalidae (both with comparatively few species). Evidence from the present work suggests that just as cydnids, and possibly acanthosomids, fly more frequently than the pentatomids, so at least some species of Alydidae and Rhopalidae fly far more than the Coreidae.

Coreidae sensu stricto

Very small numbers were taken at Kawanda, Tafo, and by Glick (1939), and none in temperate regions; yet in the tropics this family is rich in species and individuals.

Alydidae

Leptocorisa spp. were taken in light traps at Kawanda and Tafo; at the former large numbers of *Daclera punctata* Sign. were also taken.

Rhopalidae

This family does not seem to be well represented in tropical Africa; one specimen was taken at Kawanda. Glick (1939) took 17 *Liorhyssus hyalinus* (Fab.), a species that has spread round the world and is largely a migrant in Britain (Southwood and Leston, 1959).

Lygaeidae

In the tropics Lygaeidae appear to be more numerous than Miridae in light traps (Table XIV) and some species are known to be active at night (Corby, 1946). In temperate regions, however, the Blissinae and Rhyparochrominae engage in a considerable amount of diurnal flight; in southern England this is mostly post-hibernational during the first few warm days in May and, to a lesser extent, pre-hibernational in the autumn.

The Blissinae are mainly attached to Gramineae; Woodroffe (1954) observed flying macropters of *Ischnodemus sabuleti* (Fallén) in such numbers as to form a haze over Hounslow Heath, Middlesex, on 5th May, 1953. Stichel (1936) took this species every year at his veranda light in Berlin. Glick (1939) took 29 specimens of its North American counterpart, *Blissus leucopterus* (Say). Several Rhyparochrominae were taken by Glick (1939), Freeman (1939) and, mostly in the spring, during the present work (Table XVI) in suction traps. In light traps two were taken

by Thomas (1938), one by Cumber (1953) and one during this study. Glick (1939) took small numbers at night and none were caught at night in suction traps at Rothamsted (Table IX).

The Orsillinae were well represented in Glick's (1939) catches and small numbers were taken in the Rothamsted light traps (Table XVII) and one at Cardington (Table XI). Their wide distribution, especially marked in the genus *Nysius*, evinces their high powers of dispersal.

In the Heterogastrinae, *Heterogaster urticae* has been shown (p. 191) to engage in numerous short flights.

The presence of *Chilacis typhae* (Artheneinae) in both Thomas's (1938) and the present list of light trap catches is interesting. Its habitat is the heads of *Typha latifolia* and presumably flight must be essential for it to invade the new heads in late summer (Southwood and Leston, 1959). *Lygaeus equestris* (Lygaeinae) is a casual migrant to England from the Continent, and Glick (1939) records 18 specimens (four at night) of the allied *L. bicrucis* Say.

Piesmidae

In Britain *Piesma maculatum* engages in considerable post-hibernation flight activity (*see* pp. 191, 197 and Tables XV and XVI); it is, however, rarely taken in light traps (one specimen—Thomas, 1938). *P. quadratum* is a common British coastal insect and it is remarkable that this species was not captured by Freeman (1939), for on the Continent it is known to fly extensively in the spring, and Lassack (1956) has made a laboratory study of its flight behaviour. Glick (1939) took one specimen of the American *P. cinerea* (Say).

Berytinidae

Leston (1957) found that this group has a low spread potential index; this is due to the small number of rather specialised species rather than to any lack of flight activity. *Berytinus minor* has been shown to fly for over half an hour (p. 196); Glick (1939) recorded some five specimens of *Jalysus spinosus* (Say) in both the day and night catches, and took two specimens of another species over Texas (Glick, 1957). The Cyminae are now included in this family. Species of *Cymus* have been taken by Hardy and Milne (1938), Glick (1939), Freeman (1939), Southwood and Johnson (1957) and in the present study (Table XVII), but never in light traps. In Britain they engage in diurnal post-hibernation flight in late spring (early May in Southern England).

Tingidae

Some species, e.g. *Tingis cardui* (Table XVII and Southwood and Johnson, 1957) and *Corythuca* spp. (Glick, 1939), engage in considerable diurnal flight activity, in England especially after hibernation. Others, such as *T. ampliata* (H.-S.) and *Dictynota strichnocera* Fieb., which were both very common around Rothamsted but were never taken in suction traps, are obviously more static.

Reduviidae

This family is poorly represented in temperate regions; *Reduvius personatus* sometimes comes to light (Table XVII), and Glick (1939) took two species in Louisiana. Apart from the Emesinae, most Reduviids are comparatively heavy bodied insects and are therefore unlikely to be carried to considerable heights by air currents. Miller (1953) lists species taken at light in Southern Rhodesia; he says that the large subfamily Harpactorinae are mostly diurnal and only three specimens were taken at light. Other nocturnal families probably fly mostly at night, although the nocturnal

Salyavatinae have been observed flying in daylight. Males predominate over females in these captures at light and small numbers were taken at Kawanda and Tafo (Table XIV) (Southwood, 1960).

Nabidae

Perhaps the majority of temperate nabids are short-winged, but small numbers of macropterous forms were taken in aerial catches by Glick (1939), Freeman (1939) and Johnson and Southwood (1949), and in light traps by Thomas (1938), Cumber (1953) and at Tafo and Kawanda. In Britain the common fully-winged species are *Nabis ferus* and *Stalia major*; *N. rugosus* is sometimes fully-winged. Thomas (1938) took seven specimens of *S. major* but it has not been recorded in the present study. I am unable to offer an explanation of this.

N. ferus is taken in some numbers in the light traps even during the winter months. The monthly distribution of the catches is given in Table XVI and, although the bulk of the catch occurs in early autumn when the new generation has just matured, surprisingly high numbers are also taken in the months November to March; these may have walked, rather than flown, into the traps. The mirids that overwinter as adults, e.g. *Lygus rugulipennis* and *Orthops kalmi*, are not taken at this time. Nabids are known to be active at night (Fewkes, 1958), and nocturnal activity in other species of Nabidae in the early winter has been observed by Dicker (1946) and by H. F. van Emden and J. Petersen (*personal communications*) at Silwood Park, Berks. The biological significance of this hibernal activity needs elucidation.

Nabids, including members of the genera *Nabis*, *Phorticus* and *Alloeohynchus*, were taken in Kawanda and Tafo light traps (Table XIV).

Cimicidae

The Cimicinae are micropterous but many Anthocorinae and Lyctocorinae fly. The results of Glick (1939) and those in Tables IX and XI show that flight is mainly diurnal; few specimens are taken in light traps in either temperate or tropical countries.

Anthocoris confusus Reuter.—The catches of this species (Table XVI) show a post-hibernation flight in both sexes, the males dying off in May. The new generation adults are considered to appear in July, with a second generation in September (Southwood and Leston, 1959).

Anthocoris nemorum L.—In most years more females overwinter than males. The new generation adults appear in late June; the actual and flying populations fall off in late August. The second generation appears in September and both populations reach a peak in October (Southwood and Scudder, 1956), males still predominating in the catch near the ground (Table XVI).

Orius species.—Probably only females overwinter. Actual and flying populations reach a peak with the emergence of the second generation in September and early October; more males than females (Table XVI) are taken in low-level traps.

O. majusculus Reuter was recorded on two occasions by Johnson and Southwood (1949) and three *O. minutus* were caught by Freeman (1939); both species were taken at Cardington, females exceeding males (Table XI).

Lyctocoris campestris Fab. and *Xylocoris galactinus* Fieb.—These two species are inhabitants of masses of dead or decaying vegetation, *e.g.* manure heaps, grain bins, straw stacks. Both fly actively in May and June and again, in larger numbers, in August and September. Males and females were taken in equal numbers in suction traps (Table XVII).

X. galactinus was recorded at 50 and 2000 feet in August by Johnson and Southwood (1949), and both species were taken in the Ardington traps in May

(Southwood and Johnson, 1957), by Freeman (1939) and at Cardington (Table XI). Pearman (1951) observed a swarm of *L. campestris* enter a Bristol warehouse on 19th August, 1921.

Miridae

The Miridae fly more than any other family (Table XIV); the males of some species, and to a lesser extent the females also, fly at night. There are, however, considerable differences between species in the frequency and duration of flight. Details of the biology of these species are given by Southwood and Leston (1959).

Monalocoris filicis L.—Small numbers were taken in suction traps throughout the summer months (Table XVI); a remarkable feature is that the number of females exceeds that of males. This species has never been taken in light traps at Rothamsted or in Holland (Meurer 1956, 1957). As it was common in both regions and one male was taken in a suction trap at night, its absence must be due to its negative reaction to light.

Deraeocoris lutescens Sch.—Slightly more females than males were caught in suction traps; males and females were taken in May, September and October, and a solitary female in June. This species is not taken in any numbers by light traps; Thomas (1938) records two females, and in the present study three females and one male were caught in August (13th, 1949), September and October. This excess of females, which is so atypical of light trap catches of mirids, will be noted in *D. ruber*, *Lygocoris* spp. and *Calocoris norvegicus*; all these species are taken in much smaller numbers by light traps than their level of flight activity, shown by suction traps, would suggest.

Deraeocoris ruber L. Males were caught by suction traps in August and September; only one female was taken in the light traps—a remarkable situation in

TABLE XVI.—*The monthly distribution of some of the Heteroptera caught in the suction traps* (3, 3T, 4 *and* 5) *in* 1953 *and light traps* (*A*, *B*, *C and D*) *in* 1946–49. **Species of Rhyparochrominae taken*: Drymus sylvaticus, Peritrechus lundi, Taphropeltus contractus *and* Scolopostethus affinis; *numbers are given as males/females*

		Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Suction traps	Rhyparochrominae*	.	.	4/1	7/5	8/5	1/3	2/0	.	7/3	.	.	.
	Piesma maculatum (Costa)	.	.	.	.	19/17	.	.	1/0	.	.	.	.
	Anthocoris confusus Reuter	.	.	2/0	4/2	1/12	0/3	2/2	5/3	2/0	.	.	.
	A. nemorum (L.)	.	.	.	0/1	.	.	13/0	7/3	17/12	34/6	1/2	.
	Orius spp.	.	.	.	.	0/1	0/1	0/1	1/2	14/2	3/0	.	.
	Monalocoris filicis (L.)	.	.	.	.	0/1	0/1	0/2	0/1	1/1	1/0	.	.
	Heterotoma merioptera (Scop.)	.	.	.	.	.	.	.	7/1	1/0	.	.	.
	Orthotylus flavosparsus (Sahlb.)	.	.	.	.	.	1/0	1/0	13/0	46/1	14/1	.	.
Light traps	*Nabis ferus* (L.)	1/1	.	1/0	.	.	.	4/7	28/19	8/7	.	4/0	5/2
	Megalocoleus molliculus (Fall.)	.	.	.	.	.	2/0	263/14	45/0	4/0	.	.	.
	Blepharidopterus angulatus (Fall.)	.	.	.	.	.	1/0	18/0	57/19	47/13	10/0	.	.
	Orthotylus flavosparsus (Sahlb.)	.	.	.	.	.	36/0	117/13	224/52	90/31	7/0	.	.
	Lygus rugulipennis Popp.	.	.	.	.	.	33/27	890/260	310/46	143/60	3/0	.	.
	Orthops kalmi (L.)	.	.	.	1/0	.	36/8	125/4	70/5	6/1	.	.	.
	Adelphocoris lineolatus (Goeze)	.	.	.	.	.	.	168/23	485/28	57/0	.	.	.
	Stenodema calcaratum (Fall.)	.	.	.	.	.	2/1	45/3	14/2	.	.	.	.
	Trignotylus ruficornis (Geoff.)	.	.	.	.	.	4/6	18/10	20/3	5/1	.	.	.

view of the large catch of males of the closely allied but rare *D. scutellaris* Fab., the details of which have already been recorded (Southwood, 1950).

Oncotylus viridiflavus Goez.—Males were taken in light traps in July and August 1946–49, the first capture of each year being 4th August, 25th, 15th and 28th July respectively.

Megalocoleus molliculus Fall.—This was the third most abundant species (Table II) of the nine years in light trap A; it was common in all light traps in July and August (Table XVI). A single male was taken in the suction traps, at night. Thomas (1938) found—in segregated light trap catches—a marked peak of activity just before sunrise. This mirid was first taken in 1946–49 and 1956 on 12th, 3rd, 15th July, 28th June, and 8th July respectively. Nine individuals of this species were taken by Meurer (1957) in 1955, the first on 12th July.

Orthonotus rufifrons (Fall.).—A single male was taken at night in a suction trap; none was taken in light traps and, as this species was abundant in Rothamsted Manor wood, its absence from traps E_1–E_6 must be a real reflection of its reaction to light.

Harpocera thoracica Fall.—Small numbers (mostly male) were taken in May and June in Rothamsted traps, the catches of which were analysed (Table XVII). Suction trap catches also show that both sexes fly and in laboratory experiments at night both sexes flew towards an incandescent light. It is therefore difficult to explain the enormous catches of males alone by Robinson traps on certain nights. Meurer (1956) recorded 688 on 27th May, 1954 at Heemstede, Holland; previous to this 30 males and females had been taken on 24th and 25th. In contrast, the same trap took only one specimen in 1955 (Meurer, 1957). Some hundreds, all males, were caught in a Robinson trap in Rothamsted Manor wood on 20th–24th May, 1953, and Leston (*personal communication*) has noted the same phenomenon.

Plagiognathus spp. were all, except *vitellinus* (Scholtz), common at Rothamsted; none was taken in any numbers in the light traps and the results from suction traps 4 and 5 showed (p. 191) that, although *P. arbustorum* (Fab.) and *P. albipennis* Fall. engaged in numerous short flights, these were mainly in the immediate vicinity of the host plants, the males flying far more than females. Meurer (1956) comments on the absence of *P. arbustorum* from his light trap as it was very common in the locality. Thomas (1938) trapped only 4 *P. chrysanthemi* Wolff in the Rothamsted light trap 1933–36.

Asciodema obsoletum Fieber is unique in that it was the only heteropteran, taken in any numbers, that was more abundant in 1946 than in the four following years (Table XVII). The males greatly exceeded the females, but there were no catches comparable to Thomas's (1938) of 144 males in one night, small numbers being taken on several nights in late June, July and August. Thomas showed that this species was taken in a light trap at a steady rate throughout the night. The first captures each year in 1946–49, were 1st July, 24th June, 27th July and 27th June respectively.

Dicyphus spp.—Four were taken in the suction traps (Table XVII); those caught in trap 3 were all taken during the day. *D. errans* Wolff was the commonest species; it was also the only one taken in the light traps A–D and the most numerous species in light traps E_1–E_6 (Table V). It is one of the few *Dicyphus* that are always macropterous and has a wider range of host plants than most *Dicyphus* (Southwood and Leston, 1959).

D. epilobii Reuter is also always macropterous but it is restricted to one host plant; collecting showed that it was more abundant at Rothamsted than *D. errans* and thus, as it was rare in the traps, it seems that it flies less than *D. errans*. Meurer (1956) includes *D. epilobii* and other *Dicyphus* in his list of species common in the locality of his light trap but not caught. The small numbers of *Dicyphus*, especially of *D. errans*, taken in light traps E_1–E_6 contrasts with the larger numbers (Table V) of the closely allied, but relatively scarcer *Macrolophus* spp. The difference

could be due either to *Dicyphus* being entirely diurnal or simply to its not being " attracted " to light traps.

Malacocoris chlorizans Panz. was taken only at night in suction trap 3 and it is probably nocturnal in habit; only small numbers were, however, taken in the light traps.

Heterotoma merioptera (Scop.) was taken in the suction traps in some numbers, principally in August (Table XVI). It was not taken in light traps by Thomas (1938) nor in the present study, and Meurer (1956) comments on its absence from his light traps, for at Heemstede, as at Rothamsted, it was abundant in the neighbourhood.

Blepharidopterus angulatus Fall. is an active flyer; both sexes were taken in suction trap 3 during the day, whilst males were caught at night. Although exceeded in numbers by several species in Thomas's (1938) list, in both the present study and that of Meurer (1956, 1957) this was the commonest arboreal species in the light trap catches, males predominating. The majority of the catch occurs in August and September (Table XVI). The slow build-up of flying population is a reflection of the protracted hatching season of eggs (Collyer, 1952), an unusual phenomenon in overwintered mirid eggs.

Orthotylus.—Most *Orthotylus* species fly frequently. Complete identification of all species was not possible at the time but many specimens were retained and subsequently identified; complete identification was also made of the catches from traps E_1–E_6 (Table V) and H. In suction trap 3 twice as many (6 : 3) *O. ochrotrichus* (Fieber) were taken at night as in the day; *O. viridinervis* (Kirsch) and *O. tenellus* (Fall.) were also taken at night. These species, and probably several others, are partly crepuscular or nocturnal flyers. *O. marginalis* Reuter was taken in the light traps in large numbers in late June and early July and *O. virescens* (Douglas and Scott) in July and early August. Smaller numbers of *O. diaphanus* (Kirsch) were caught in late July and August and of *O. nassatus* (F.) in August. Both these species were taken by Meurer (1957) in some numbers. The bulk of the unidentified material was caught in July and probably represented a mixture of *O. ochrotichus* and *O. prasinus* (Fall.). Small numbers of *O. concolor* (Kirsch) were taken in trap H (1955) and single specimens of *O. adenocarpi* (Perris) in trap E_1 and of *O. ericetorum* in trap B.

Orthotylus flavosparsus (Sahl.) is easily distinguished from all other *Orthotylus* species; it was separated throughout the work and was the fourth most abundant species of Heteroptera (Table II). The monthly flight activity in light and suction traps is shown in Table XVI. Small numbers fly in June and these are the first generation; the largest numbers, the second generation, are caught in late July or August. The first records in 1946–49 and 1956 were 14th, 1st, 27th, 27th and 21st June respectively. The only specimen caught in trap 3 was taken during the day; Thomas (1938) found that the greater part of the light trap catch was made just before sunrise. Meurer (1956, 1957) and Frost (1952) also took numbers of this species in their light traps.

Lygus spp. fly frequently. In the U.S.A. *L. lineolaris* P. de B. was taken in large numbers by Glick (1939) in aeroplane traps and by Frost (1953) in light traps (Table XV). In Western Europe the commonest species is *L. rugulipennis* Poppius (Southwood, 1956); Johnson and Southwood (1949) found that it greatly exceeded all others in catches between 50 and 3000 feet and it was the most abundant species in the light trap catches of Thomas (1938) and in the present study. It overwinters as an adult, but the overwintered adults are seldom taken in light traps in the spring; the only example was one female on 6th June, 1956. The earliest records, due to the new first generation, for 1946–49 and 1956 were 3rd July, 26th, 25th, 27th June and 7th July respectively. The monthly distribution in the light traps is given in Table XVI; the large July total compared with that for August is mainly due to the 1948

figures (p. 176). Johnson and Southwood's (1949) figures and field observations show that the second generation, produced in September, is more numerous than the first and the individuals fly as much if not more. The reason why this generation is so poorly represented in the light trap catches is probably that flight in *L. rugulipennis* is more diurnal than nocturnal, and, because of the low night temperatures in September, the proportion of nocturnal or crepuscular flight is still further reduced. The evidence for the preponderance of diurnal flight is that all those taken in trap 3 (Table IX) and the Cardington traps (Table XI) were taken during the day, whilst Thomas (1938) found that the light trap catches had a large peak at the beginning of the night and a smaller one just before sunrise. The relation of light trap catches to temperature in this species has been analysed (p. 185).

Liocoris tripustulatus (Fab.) flies very seldom. This contrasts with *Lygus*, a genus in which it is sometimes placed. Although abundant at Rothamsted, it was never taken in the light traps or in the suction traps, even when a large population was adjacent (Table XII). It was not recorded by Thomas (1938) or by Meurer (1956, 1957), who comments on its absence. That it does occasionally fly is evidenced by Johnson and Southwood's (1949) record of a single specimen at 50 feet.

Orthops cervinus H.-S. is an arboreal species ; it is remarkable in that over twice as many females as males were taken in suction traps (Table XVII) ; one of the females was taken at night in trap 3. Small numbers were taken by Thomas (1938), and Meurer (1956, 1957) took only one specimen in 1954, but 17 in 1955; similar fluctuations were noted in the present study (Table XVII). The majority of specimens were taken in trap B, which was close to a number of lime (*Tilia*) trees.

Orthops campestris L. is as abundant as *O. kalmi* at Rothamsted, yet only one female was taken in the light traps and it was not caught by Thomas (1938). This is a reflection of a low level of flight activity, for it was not present in the suction trap catches and was found in smaller numbers than *O. kalmi* at Cardington (Johnson and Southwood, 1949 ; and Table XI).

Orthops kalmi L. overwinters as an adult. It shows a very high level of flight activity (Johnson and Southwood, 1949, and Tables II, XI, XV and XVII); it has been taken in suction traps at Cardington at night, but in smaller numbers than during the day. The monthly distribution of catches in light traps is shown in Table XVI. The earliest records for the adults in 1946–49 and 1956 were 7th July, 24th June, 24th July, 26th June and 8th July respectively. Although males predominate in light trap catches, the sexes are virtually equally represented in suction trap samples (Tables XI and XVII). This species feeds on a wide range of umbelliferous plants, whilst the closely allied *O. campestris* is more restricted ; nevertheless the greatly differing levels of flight activity in the two are remarkable.

Lygocoris spp. were taken in comparatively moderate numbers in the suction traps and in small numbers in the light traps. *L. viridis* Fall., at least, is active at night, for it was present in the night catches from trap 3, and it would seem that the Rothamsted traps were not suitable for their capture, for Thomas also records very few. In contrast Meurer (1956, 1957) took large numbers of *L. pabulinus* L. Frost (1952) remarks how the related nearctic *L. communis* Knight was taken only in light traps close to the host tree, whilst in the present work *L. lucorum* was represented (by 4 specimens) in suction trap 5 near its host plants, nettle (*Urtica*) and mugwort (*Artemesia vulgaris*), and absent from the nearby trap 4. Thus it is probable that flight is generally short and their behaviour is such that they are not commonly caught in light traps with a closed top and an incandescent bulb.

Calocoris sexguttatus Fab. was very abundant in Rothamsted Manor Wood, and it is noteworthy that it was not taken in light traps E_1–E_6 or in suction trap 7 (Table XII).

Calocoris norvegicus Gmelin is a common mirid with a large number of host plants. Table XII suggests that it has quite a high level of flight activity, yet it was poorly

represented in the light trap catches (Table XVII); both Thomas (1938) and Meurer (1956) have commented on its paucity or absence in their catches. Cumber (1953) took one specimen in New Zealand. The failure of light traps to catch this species may be because it flies only by day (it was absent from the night catches of trap 3) or possibly because of its reaction to light.

Adelphocoris lineolatus Goez. was the second most abundant species in the Rothamsted light traps (Table II) and was the only non-woodland bug represented in the majority of the E series of traps (Table V); suction traps, however, do not show it to have such a high level of flight activity (*see also* p. 192). Now Thomas's (1938) data show that *A. lineolatus* was unique amongst the seven common mirids, whose times of capture by the light trap were analysed, in that it had a peak just after midnight and minima at sunset and sunrise. Thus it may be that most of the flight activity of *A. lineolatus* is nocturnal, which would explain the high light trap catches *vis-à-vis* those of suction traps. The monthly distribution of this species is given in Table XVI; it was first captured in 1946–49 and 1956 on 12th, 6th, 18th, 22nd and 26th July respectively.

Stenotus binotatus Fab. was one of the more abundant species in the catches of the Rothamsted light traps (Table II); in New Zealand, Cumber (1953) found that the major part of a year's catch consisted of this mirid. The catches at Rothamsted consisted entirely of males (Thomas, 1938, and Table XVII), which were taken in suction trap 3 by day and by night. Males flew readily for a minute or less in the laboratory after sunset on 16th July, but females could not be induced to do so. Females, nevertheless, do fly, and one was taken in suction trap 7; their flight activity is, however, low and that of the males high. It seems that males fly considerably at night and Thomas (1938) found that almost equal numbers were taken at all periods throughout the night. The period of adult life is short and the monthly distribution of light trap catches is shown in Table XVII; the first records in 1946–49 were 9th July, 24th June, 18th July and 27th June respectively.

Phytocoris spp.—Some species of this genus may be mainly nocturnal, for *P. tiliae* F. and *P. dimidiatus* (Kirsch.) were found more often at night than during the day in suction trap 3. The aboreal *Phytocoris* are taken in small numbers in light traps throughout July, August, September and October; this long adult period, similar to that of *Blepharidopterus angulatus* (*q.v.*), is probably a reflection of the protracted hatching period which is known to occur in *P. tiliae*. The earliest records of *P. varipes* Boheman in 1946–49 and 1955 were 22nd, 19th July, 2nd August, 23rd July and 1st August respectively.

Capsus ater L. would seem, from the evidence given in Table XII, and from its absence from all light and suction trap catches, to fly but seldom. However, Frost (1953) mentions it as occurring regularly in his light traps in Pennsylvania; it may be that this is really a different species or more probably that the species has different levels of flight activity in different parts of its range.

The tribe Stenodemini, or grass bugs, show interesting variations in the amount of flight activity which appear to be correlated with the type of habitat. *Megalocera recticornis* (Geoff.) was common at Rothamsted but was never taken in any of the traps; *Notostira elongata* Geoff. was also not recorded, but was less common and therefore it cannot be said with such certainty that it has a low level of flight activity. Slightly more flight activity was found in *Leptopterna dolabrata* L. and *Stenodema laevigatum* L.; indeed field observations (Table XIII) showed that the latter engaged in numerous mainly short flights, yet its aerial density was less than that of *S. calcaratum* Fall. (Table XII), whose population level was certainly no higher. The highest level of all was found in *Trignotylus ruficornis* (Geoff.), the large light trap catches of which may have been partly due to its more nocturnal habits, although Glick (1939) took large numbers of the closely allied *T. brevirostris* (Table XV) during the day. Collecting showed *T. ruficornis* to be the least abundant of the Stenodemini at Rothamsted.

TABLE XVII.—*The Heteroptera caught in various light and suction traps at Rothamsted Experimental Station, Harpenden.* (*Light traps A–D and H, suction traps* 1–7; *for results from other light traps see Tables VII and VIII; for details of the Corixidae see Brown*, 1954; — *is equivalent to zero*)

	Light traps					All years			Suction traps (1–7)		
	1946 A, B, C	1947 A, B, C	1948 A, B, D	1949 A, B, D	1956 H	♂♂	♀♀	Total	♂♂	♀♀	Total
ARADIDAE . . . total	.	.	.	.	.	.	.	.	1	1	2
Aradus depressus (Fab.)	—	—	—	—	—	—	—	—	1	1	2
ACANTHOSOMIDAE . . . total	.	.	.	.	.	1	3	4	.	.	.
Acanthosoma haemorrhoidale (L.)	—	2	—	1	—	1	2	3	—	—	—
Elasmostethus interstinctus (L.)	.	.	.	1	.	.	1	1	—	—	—
PENTATOMIDAE . . . total	.	.	.	.	.	18	.	18	.	.	.
Pentatoma rufipes (L.)	1	7	—	10	—	18	—	18	—	—	—
LYGAEIDAE . . . total	.	.	.	.	.	9	2	11	83	27	110
Heterogaster urticae (Fab.)	—	—	—	—	—	—	—	—	53	11	64
Chilacis typhae (Perris)	—	—	1	5	—	5	1	6	—	—	—
Nysius thymi (Wolff)	—	—	—	1	—	—	1	1	—	—	—
Kleidocerys resedae (Panzer)	—	1	—	—	—	1	—	1	—	—	—
K. truncatulus (Walker)	1	1	—	—	—	2	—	2	—	—	—
Peritrechus lundi (Gmelin)	—	—	—	—	—	—	—	—	2	1	3
Drymus sylvaticus (Fab.)	—	—	1	—	—	1	—	1	19	8	27
Scolopostethus affinis (Schilling)	—	—	—	—	—	—	—	—	2	1	3
Taphropeltus contractus (H.-S.)	—	—	—	—	—	—	—	—	7	6	13
BERYTINIDAE . . . total	.	.	.	.	.	.	.	.	1	.	1
Cymus claviculus (Fall.)	—	—	—	—	—	—	—	—	1	—	1
PIESMIDAE . . . total	.	.	.	.	.	.	.	.	21	18	39
Piesma maculatum (Costa)	—	—	—	—	—	—	—	—	21	18	39
TINGIDAE . . . total	.	.	.	.	.	.	.	.	2	3	5
Derephysia foliacea (Fall.)	—	—	—	—	—	—	—	—	1	—	1
Tingis cardui (L.)	—	—	—	—	—	—	—	—	1	3	4
REDUVIIDAE . . . total	.	.	.	.	.	1	.	1	.	.	.
Reduvius personatus (L.)	—	—	1	—	—	1	—	1	—	—	—
NABIDAE . . . total	.	.	.	.	.	46	44	90	3	3	6
Nabis ferus (L.)	—	23	3	61	—	46	41	87	3	2	5
N. rugosus (L.)	—	—	—	3	—	—	3	3	—	—	—
Dolichonabis limbatus (Dahlb.)	—	—	—	—	—	—	—	—	—	1	1
CIMICIDAE . . . total	.	.	.	.	.	3	11	14	127	79	206
Anthocoris confusus Reuter	1	—	1	—	—	1	1	2	17	27	44
A. nemoralis (Fab.)	—	—	—	—	—	—	—	—	—	7	7
A. gallarum-ulmi (De Geer)	—	—	—	—	—	—	—	—	—	1	1
A. nemorum (L.)	—	2	1	2	2	1	6	7	82	28	110
Acompocoris pygmaeus (Fall.)	—	—	—	—	—	—	—	—	2		2
Orius majusculus Reuter	—	—	—	—	1	1	—	1	4	5	9
O. minutus (L.)	—	—	—	—	—	—	—	—	11	3	14
O. niger (Wolff)	—	—	—	—	—	—	—	—	5	1	6
Lyctocoris campestris (Fab.)	—	4	—	—	—	—	4	4	3	3	6
Xylocoris galactinus (Fieber)	—	—	—	—	—	—	—	—	3	4	7
MICROPHYSIDAE . . . total	.	.	.	.	.	1	.	1	2	.	2
Loricula elegantula (Baerensp.)	—	—	—	1	—	1	—	1	2	—	2
MIRIDAE . . . total	.	.	.	.	.	4873	868	5741	386	141	527
Monalocoris filicis (L.)	—	—	—	—	—	—	—	—	2	6	8
Deraeocoris lutescens (Sch.)	1	1	1	1	—	1	3	4	7	9	16
D. ruber (L.)	—	—	1	—	—	—	1	1	8	—	8
D. scutellaris (Fab.)	3	5	9	2	—	19	—	19	—	—	—
Lopus decolor (Fall.)	1	—	—	1	—	2	—	2	—	—	—
Oncotylus viridiflavus (Goeze)	1	6	2	7	—	16	—	16	—	—	—

TABLE XVII.—*continued*

	Light traps					All years			Suction traps (1–7)		
	1946 A, B, C	1947 A, B, C	1948 A, B, D	1949 A, B, D	1956 H	♂♂	♀♀	Total	♂♂	♀♀	Total
Megalocoleus molliculus (Fall.)	23	111	116	78	21	335	14	349	1	—	1
Macrotylus solitarius (Mey.-Dür.)	1	12	28	23	—	63	1	64	1	—	1
Orthonotus rufifrons (Fall.)	—	—	—	—	—	—	—	—	1	—	1
Harpocera thoracica (Fall.)	1	1	8	—	1	10	1	11	7	5	12
Brachyarthrum limitatum Fieb.	1	—	—	—	—	1	—	1	—	—	—
Phylus melanocephalus (L.)	—	2	—	1	—	3	—	3	—	—	—
P. coryli (L.)	1	—	—	—	—	1	—	1	—	1	1
Plesiodema pinetellum (Zett.)	—	3	—	—	—	3	—	3	—	1	1
Psallus—all species	13	32	19	31	.	76	19	95	.	.	.
P. ambiguus (Fall.)	.	.	.	.	.	.	.	.	—	2	2
P. perrisi Wag. group	.	.	.	.	1	1	.	1	48	11	59
P. roseus (Fab.)	.	.	.	.	.	.	.	.	—	1	1
P. varians (H.-S.) and *P. diminutus* (Kirsch)	.	.	.	.	3	3	.	3	13	2	15
P. obscurellus (Fall.)	.	.	.	.	.	.	.	.	—	5	5
P. salicellus (H.-S.)	.	.	.	.	.	.	.	.	3	—	3
Atractotomus mali (Mey.-Dür.)	—	—	—	—	—	—	—	—	—	1	1
A. magnicornis (Fall.)	1	—	6	4	—	11	—	11	7	2	9
Plagiognathus albipennis (Fall.)	—	4	—	1	—	5	—	5	9	—	9
P. arbustorum (Fab.)	—	—	—	1	—	1	—	1	34	6	40
P. chrysanthemi (Wolff)	—	2	2	1	—	5	—	5	1	1	2
Campylomma verbasci (Mey.-Dür.)	—	2	—	7	—	6	3	9	—	—	—
Sthenarus roseri (H.-S.)	—	—	1	—	—	1	—	1	—	—	—
S. rotermundi (Scholtz)	—	3	—	—	—	2	1	3	—	—	—
Asciodema obsoletum Fieber	46	8	10	21	—	82	3	85	—	—	—
Macrolophus spp.	—	1	—	1	—	2	—	2	—	—	—
Dicyphus epilobii Reuter	—	—	—	—	—	—	—	—	—	1	1
D. errans (Wolff)	—	—	—	1	—	1	—	1	—	3	3
D. stachydis Reuter	—	—	—	—	—	—	—	—	1	—	1
D. pallidicornis (Mey.-Dür.)	—	—	—	—	—	—	—	—	—	1	1
Campyloneura virgula (H.-S.)	—	—	—	2	—	—	2	2	—	—	—
Pilophorus cinnamopterus (Kirsch)	—	—	—	1	—	—	1	1	—	—	—
Orthocephalus saltator (Hahn)	3	1	1	1	—	6	—	6	—	—	—
Malacocoris chlorizans (Panz.)	—	2	—	5	—	7	—	7	2	—	2
Cyllecoris histronicus (L.)	—	1	—	—	—	1	—	1	1	1	2
Dryophilocoris flavoquadrimaculatus (De Geer)	—	3	—	—	—	3	—	3	3	1	4
Globiceps flavomaculatus (Fab.)	—	—	1	—	—	1	—	1	—	—	—
Heterotoma merioptera (Scop.)	—	—	—	—	—	—	—	—	8	1	9
Blepharidopterus angulatus (Fall.)	19	33	18	88	—	125	33	158	5	2	7
Pachylops bicolor (Doug. and Scott)	2	7	2	1	—	12	—	12	1	—	1
Orthotylus spp. (see pp. 176 and 207)	17	58	67	125	.	232	35	267	.	.	.
O. tenellus (Fall.)	.	.	.	.	—	.	.	.	1	1	2
O. viridinervis (Kirsch)	.	.	.	.	—	.	.	.	5	—	5
O. marginalis Reut.	.	.	.	.	2	2	.	2	1	1	2
O. ochrotrichus Fieb.	.	.	.	.	—	.	.	.	17	3	20
O. prasinus (Fall.)	.	.	.	.	—	.	.	.	1	—	1
O. virescens (Doug. and Scott)	.	.	.	.	1	1	.	1	1	—	1
O. flavosparsus (Sahlb.)	40	412	19	159	27	560	97	657	83	8	91
Pseudoloxops coccineus (Mey.-Dür.)	—	2	1	13	2	11	7	18	3	—	3
Mecomma ambulans (Fall.)	—	—	—	—	—	—	—	—	5	—	5
Lygus pratensis (L.)	1	—	2	1	—	4	—	4	—	—	—
L. rugulipennis Popp.	142	718	743	168	436	1744	463	2207	21	8	29
Orthops rubricatus (Fall.)	—	—	—	—	—	—	—	—	3	—	3
O. cervinus (H.-S.)	51	55	7	94	1	150	58	208	9	19	28
O. campestris (L.)	—	1	—	—	—	—	1	1	—	1	1
O. kalmi (L.)	45	111	22	78	20	257	19	276	5	2	7
Lygocoris pabulinus (L.)	1	3	—	5	1	5	5	10	6	—	6
L. viridis (Fall.)	—	2	—	—	—	2	—	2	3	2	5
L. contaminatus (Fall.)	—	3	6	3	—	5	7	12	1	1	2

TABLE XVII.—*continued*

	Light traps					All years			Suction traps (1–7)		
	1946 A, B, C	1947 A, B, C	1948 A, B, D	1949 A, B, D	1956 H	♂♂	♀♀	Total	♂♂	♀♀	Total
L. spinolai (Mey.-Dür)	—	—	—	—	—	—	—	—	4	1	5
L. lucorum (Mey.-Dür)	—	1	—	—	—	1	—	1	15	4	19
Plesiocoris rugicollis (Fall.)	—	2	—	—	—	2	—	2	—	—	—
Polymerus unifasciatus (Fab.)	—	—	1	—	—	1	—	1	—	—	—
P. nigritus (Fall.)	—	—	6	—	—	6	—	6	—	—	—
Calocoris quadripunctatus (Villess.)	—	2	—	—	—	2	—	2	1	—	1
C. norvegicus (Gmelin)	2	—	9	—	—	6	5	11	15	18	33
Adelphocoris lineolatus (Goeze)	206	206	108	242	12	722	52	774	1	—	1
Megacoelum infusum (H.-S.)	1	—	1	—	—	1	1	2	—	—	—
Stenotus binotatus (Fab.)	4	41	26	18	—	89	—	89	4	1	5
Phytocoris tiliae (Fab.)	9	6	3	23	—	35	6	41	5	2	7
P. dimidiatus Kirsch	—	9	1	2	—	12	—	12	3	—	3
P. longipennis Flor	1	—	—	2	—	3	—	3	—	—	—
P. reuteri Saunders	—	7	—	13	—	15	5	20	—	2	2
P. ulmi (L.)	—	1	1	3	—	5	—	5	—	—	—
P. varipes Boheman	10	47	9	13	1	77	3	80	2	—	2
Pantilius tunicatus (Fab.)	—	2	—	—	—	2	—	2	—	—	—
Stenodema calcaratum (Fall.)	6	23	33	5	3	64	6	70	3	1	4
S. laevigatum (L.)	—	—	—	2	—	1	1	2	2	1	3
Trignotylus ruficornis (Geoff.)	9	40	2	10	4	50	15	65	1	0	1
Leptopterna ferrugata (Fall.)	—	1	—	—	—	1	—	1	—	—	—
L. dolabrata (L.)	—	—	—	—	—	—	—	—	2	2	4
SALDIDAE . . . total	.	.	.	.	.	.	.	.	2	.	2
Saldula orthochila (Fieb.)	—	—	—	—	—	—	—	—	2	—	2
CORIXIDAE . . . total	2	2	—	8	—	5	7	12	—	—	—
Unidentified	1	3	1	—	—	3	2	5	.	.	.
Totals	668	2038	1301	1351	539	4960	937	5897	628	272	900

It is noteworthy, and perhaps significant, that *M. recticornis* is dominant in damp undisturbed grassland, and *L. dolabrata*, *S. laevigatum* and *S. calcaratum* occupy a series of intermediate positions on a gradient towards drier conditions. Under the driest conditions, *T. ruficornis* becomes dominant. This species and *S. calcaratum* are also dominant in salt marshes. Thus the series of species arranged according to increasing flight activity reflects that based on increasing aridity of the habitat. The monthly distribution of the catches of *S. calcaratum* and *T. ruficornis* are given in Table XVI.

(2) *General Conclusions*

(a) *The Relation of Flight Activity to the Habitat, more especially the Host Plant*

On *a priori* grounds it might be expected that the amount of flight activity of the type likely to lead to dispersal (*i.e.* not flits, p. 197) in a given species would be related to the frequency with which the individuals are compelled to find a new "place to live". Southwood and Scudder (1957) had evidence that suggested that in the thistle lace bugs, *Tingis cardui* and *T. ampliata*, the former, which is attached to a biennial host, shows more flight activity than the latter, whose host plant is a perennial. Haine (1955), working with aphids, showed that tree dwelling species took off less readily under unfavourable conditions ("high" wind speeds) than those with an alternation of generations (*i.e.* temporary habitats). Brown (1951) has already discussed the relationship between migration rate and type of habitat in the Corixidae.

With the terrestrial Heteroptera, therefore, one would expect the highest levels of flight activity in species that live in temporary habitats. These may be annual,

biennial or short-lived host plants or, in the case of some predators, flowers or decaying vegetation.

The most abundant species in most of the various traps in different countries are given in Table XV; this abundance is a reflection of both the level of flight activity and the actual size of the population. Only in the small experiment described on p. 193 have the two factors been separated, and the penultimate column in the table gives the species (present in that habitat) shown to have a high level of flight activity.

Of the 20 species, or allied species, in Table XV, 16 are inhabitants of temporary habitats and, of the exceptions, only *Trignotylus* species are taken at all regularly. They are bugs of dry areas attached to various grasses, whilst *Plagiognathus arbustorum* engages in short flits (p. 206) rather than the type of flight likely to lead to dispersal. *Stenotus binotatus*, not included in Table XVI, is another abundant species in light trap catches, but only males are taken, suggesting that most flights are short flits (Table XVII; Cumber, 1953; Frost, 1952).

The majority of the species in Table XV feed on "weeds". It is noteworthy that one of the most abundant and, at the same time, most temporary of heteropterous host plants is *Chenopodium album*; the bugs almost confined to it are *Piesma maculatum* and *Orthotylus flavosparsus*, whilst it is an important host of the polyphagous *Lygus* species. This excess of "weed" species is unlikely to be due to the habitats, for Glick (1939) collected over predominantly forest and swamp areas in Louisiana and several of Frost's (1952) 18 traps were in woodland conditions. There are also many trees and grass leys in the grounds at Rothamsted, Harpenden (fig. 1), whilst at Cardington, and probably elsewhere, grass is the dominant ground vegetation. There seems, therefore, to be no reason to suppose that in these areas the populations of the weed inhabitating Heteroptera would greatly exceed those of both grass and tree species, as they do in Tables IV and XV. Other examples of temporary habitats are flowers (*Orius insiduosus*), manure heaps and vegetation refuse (*Lyctocoris campestris* and *Xylocoris galactinus*).

Species with a wide range of host plants may fly more than closely allied ones with more restricted habitats. In *Dicyphus* (p. 206) the more predatory species with a wide range of host plants show more flight activity than the more phytophagous species with a single host plant. A similar situation occurs in *Orthops* (p. 208) where, however, both species are phytophagous. *Anthocoris nemorum*, considered to be a "permanent habitat species" in Table XV, is a predator that may be found on almost any plant.

The last type of relationship is found in the grass-dwelling Stenodemini, the commoner British species of which may be arranged (p. 209) in series of increasing flight activity and increasing aridity of the habitat; these two series correspond exactly.

We may conclude that those terrestrial Heteroptera that show a high level of flight activity are mainly associated with temporary habitats. There is also a suggestion that species with a large number of host plants fly more than closely allied species with a single host plant—provided that the hosts are all the same type of plant (*e.g.* perennials).

(b) *The Relation of Catch Size in Different Years to the Type of Host Plant*

There is some association between host plant and abundance of Heteroptera in light trap catches in different years, for, if the annual totals of the various major grass and arboreal species taken over the four years 1946–49 are plotted (fig. 3), it will be seen that the grass species were most abundant in 1947 and the arboreal species in 1949. The only exceptions are the grassland *Stenodema calcaratum*, most abundant in 1948, and the arboreal *Psallus*, which was just more abundant in 1947 than in 1949. It would be unwise, for the reasons outlined in the introduction,

to claim that there were higher populations of grass species in 1947 than in 1949, and the reverse for the arboreal species. The increase may have been entirely due to increased flight activity or a combination of the population and activity. Both 1947 and 1949 were hot, dry years, and it is possible that in 1947 the hot weather increased

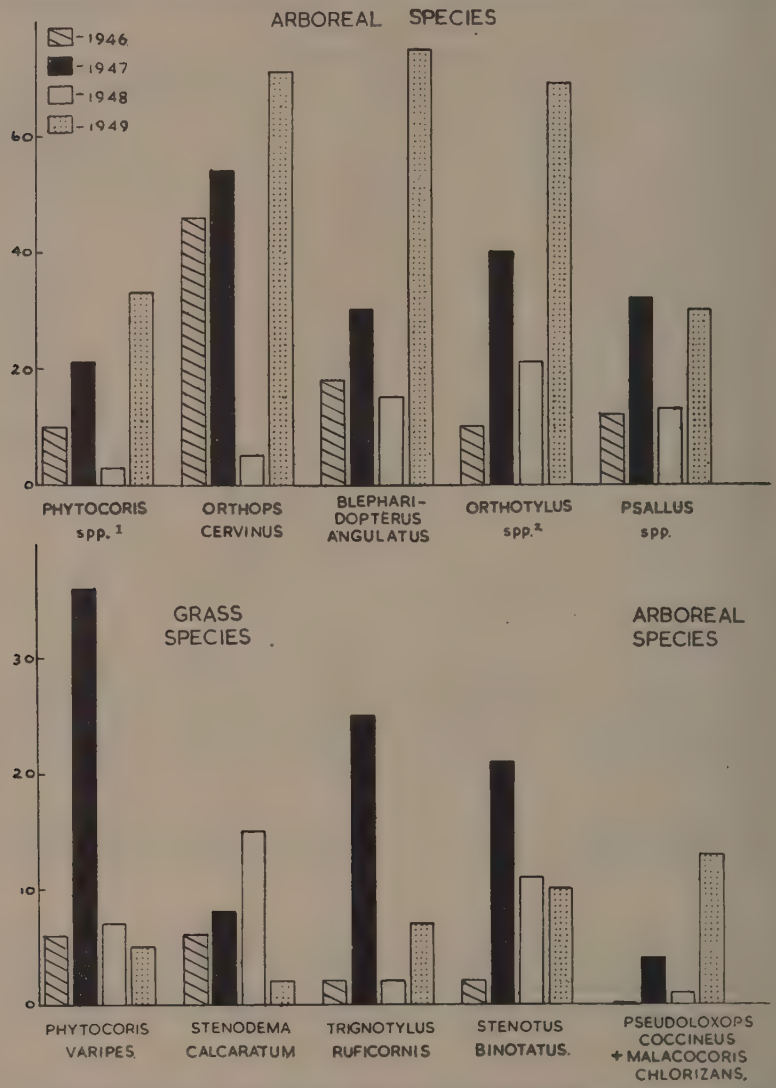

FIG. 3.—Histograms of the numbers of various arboreal and grassland Heteroptera taken in light traps at Rothamsted in each of the four years 1946–49. ([1]*Phytocoris* spp., excluding *P. varipes* ; [2]*Orthotylus* spp. = subgenus *Orthotylus*, less *O. adenocarpi* group.)

the frequency of flight of all species ; the same could have happened in 1949 but, as this year was even drier, the populations of the grass species were reduced because of the effect of the drought on their hosts. It is noteworthy, however, that Johnson and Eastop (1951) found large numbers of grass aphids in suction trap catches in 1947, and Strickland (1958) records 1947 as a year of especially heavy attack by the

frit fly, *Oscinella frit*, a stem-borer of Gramineae ; whilst Varley and Gradwell (1958) found that 1949, the year they started sampling, was one of the years when there were large populations of oak tree caterpillars.

(c) *Comparative Account of Flight and Dispersal in the Different Families*

Leston (1957) has devised the spread potential index of a taxon ; this is an expression of the relative ability of taxa to disperse and colonise, and is obtained by considering the numbers of original immigrant species of each taxon in the fauna of various oceanic islands. The taxon with the most representatives (in this case the Miridae) is allotted an arbitrary value of 100 and the others are calculated in proportion to this.

The value for spread potential is a reflection of both the flight activity of the members of the taxa—in this case the families of Heteroptera—and also of their numerical abundance. Indeed a family with a large number of abundant species capable of occupying a wide range of ecological niches has a greater potentiality for spread than a much smaller family, even if the members of both exhibit a similar amount of flight activity. Leston found that the taxa with the highest spread potentials were : Miridae (100), Lygaeidae (60), Pentatomoidea (including Cydnidae) (36), Emesinae (30) and Cimicidae (excluding Cimicinae) (26). The first three groups probably have something approximating to the same number of species and thus their spread potential values should be a comparison of flight activity. They bear a remarkable similarity to the values in Table XIV, and therefore the two independent studies strongly support each other's conclusions.

At this point it should perhaps be stressed that not all types of flight activity are equally likely to lead to dispersal. Extremely short flights—flits (p. 197)—as found in *Plagiognathus arbustorum*, would be less likely to lead to dispersal than the longer flights. Dispersal may be achieved by active flight alone or a combination of this and passive carriage by air currents. The likelihood of the latter will depend on the time of flight—both season and day—and on other factors. It would seem that in England the heavy fast-flying lygaeids and cydnids, whose main flight period is in late spring, would be less likely to be carried into upper air than the generally weaker mirids, whose main flight period moreover is in the summer months. Freeman (1945), writing on the distribution of insects by aerial currents, says " certain groups are only likely to be dispersed short distances, since they show a very high proportion of the total catch in the nets of the lowest level ; such families are . . . and most Heteroptera ". An examination of his data (Freeman, 1939) shows that this applies to *Piesma* and other lygaeoids, but not to mirids.

Johnson (1957) has worked out an empirical relation of density to height. The differences alluded to here should be shown quantitatively in a lower value of λ for his equation with the Miridae than with the lygaeoid and pentatomoid families. At present the necessary data are not available.

Hence the evidence from the present study supports Leston's (1957) theory that the Miridae and Lygaeidae have high spread potentials. The lower spread potential of the Cimicidae (excluding Cimicinae) and the absence of one for the Piesmidae are due to the smaller numbers of species and not to lower flight activity. In contrast, the low value (6) for the Coreidae is probably a reflection of a very low level of flight activity (see p. 202).

(d) *Some Characteristics of the Flight Activity of Heteroptera in Comparison with Other Insects*

It has already been pointed out in the introduction that the Heteroptera belong to that group of insects in which walking, not flying, is the primary means of locomotion (*vide* Southwood and Johnson, 1957) and therefore, in comparison with

a dipteron, for instance, a bug is likely to spend a relatively small amount of its life in flight. It has also been shown (p. 197) how in temperate countries pre- and, to a greater extent, post-hibernation flight may be frequent and with quite a considerable range in many lygaeoids and others, such as *Tingis cardui* and *Sehirus bicolor*.

In the majority of species, however, the flight range is evidently small; this is reflected in the different indices of diversity for the Heteroptera taken in the various Rothamsted traps, even when they were only 10 yards apart (traps 4 and 5, Table X). This contrasts strongly with Williams's (1950) findings that Lepidoptera sampled by all the light traps at Rothamsted came from the same population and with Banks's (1959) data for the Syrphidae, where, although the indices of diversity of the catches—and hence the populations—of the more distant ($\frac{1}{4}$ mile apart) traps differed, those of traps 4 and 5 were identical. These groups obviously have far greater mean flight ranges.

Heteropteran flight activity in temperate regions is primarily diurnal (p. 189) and Thomas's (1938) data show that the majority of species taken in numbers in light traps have peaks near dusk and dawn (although certain species, e.g. *Phytocoris spp.*, *Adelphocoris lineolatus* and others (*see* section IV(1)), appear to be mainly crepuscular or nocturnal).

It has been shown (p. 183) that the sizes of the total catch of Heteroptera and of a single species, in the Rothamsted light traps, are more closely associated with maximum than with minimum temperature. Broadbent (1947) found this was the case with the Aphididae taken in light traps, although Robertson (1939), working with Tipulidae and Williams (1940) with Lepidoptera and total insects, found the closest association between catch size and minimum temperature, which is of course a nocturnal temperature, usually sometime just before dawn. The explanation would seem to be that, whilst the Heteroptera and Aphididae are primarily diurnal groups, the Tipulidae and the Lepidoptera (at least those taken in light traps) are almost entirely nocturnal.

An alternative, or perhaps complementary explanation, for the two are by no means mutually exclusive, is that, because the mean flight threshold of Heteroptera (*c.* 19° C.) is higher than that of most Lepidoptera and Diptera Nematocera (which made up the majority of the catches analysed by Williams (1940)), the minimum temperature may often be below their flight threshold. In fact Williams (1940 : 265) states " that maximum temperatures may have a greater importance in years of low maxima than in years of high maxima ". This is, of course, the same principle but with the temperature considered as the variable rather than the insect group.

Summary

1. Details are given of the Heteroptera taken in various light and suction traps at Rothamsted Experimental Station, Harpenden, some of which ran for several years, and also from shorter periods of trapping at Kawanda (Uganda) and Tafo (Ghana); and with suction traps at different heights at Cardington, Beds.

2. With light trap catches at Harpenden it is shown that almost all the Heteroptera are caught from June to September, but that the daily distribution of the catch is dependent on the number of days with a maximum temperature of 75° F. or more. It is shown that with Heteroptera there is more correlation between total catch and maximum temperature, than between it and minimum temperature; this is interpreted as being a reflection of the mainly diurnal flight of most Heteroptera and of their high flight temperature thresholds in contrast to many Diptera and Lepidoptera. The regression equation of maximum temperature on total catch for 340 nights is such that the catch would be zero on days with a maximum of 59° F. or below,

and 10 at 75° F.; the catch is doubled by a rise of 4·9° F. in the maximum temperature.

3. The Robinson-type light trap catches more terrestrial Heteroptera and far more Corixidae, largely because of its open top design rather than its ultra-violet light. It increases the proportion of males in the catches of both Miridae and Corixidae.

4. Comparisons between the different traps show that each catch is largely dependent on its immediate surroundings and the samples of Heteroptera taken in most traps at Rothamsted have distinct indices of diversity which contrast with the identical ones for the Lepidoptera taken in the same light traps (Williams, 1950). This fact, and field and laboratory observations, have led to the conclusion that in many species of Heteroptera, more especially of Miridae, the majority of the flights are " flits " of short duration. Other Heteroptera, such as *Piesma maculata* Castelnau, were taken in most suction traps and were found to be capable of flights of a duration of an hour or so, sometimes much longer.

5. The comparison of light and suction trap catches showed that the majority of heteropteran flight in England is diurnal, in the Lygaeoid families apparently entirely so. The Miridae dominated the suction trap catches at night, as they do those of light traps.

6. Flight activity is almost equal in both sexes of most lygaeoids and nabids; males engage in more flight activity in anthocorids (Cimicidae) and in most mirids, but there are certain exceptions. An extremely high proportion of males in a catch of a certain species appears to be associated with numerous flights of short duration—flits, the majority of which will not lead to dispersal.

7. An account is given of an experiment in which the catches of a suction trap are compared with simultaneous samples of the actual populations in the surrounding area. It indicates very different levels of flight activity in different species.

8. The catches made at Rothamsted are compared with those made elsewhere in Britain and in Holland, southern and northern U.S.A., Mexico, New Zealand, Uganda and Ghana. Basically similar patterns of families and—in the temperate countries—of abundant species are demonstrated.

9. It is pointed out that those species with high levels of flight activity are inhabitants of temporary habitats (*e.g.* annual host plants, dry biotopes).

10. A comparison of the numbers of arboreal and grass-dwelling species taken in light traps in the years 1946–49 shows that the highest figures for most grassland species were in 1947 and for arboreal in 1949. These are paralleled by independent observations on other groups in these habitats.

11. Flight activity is considered in relation to dispersal from the zoogeographical angle, and it is shown that the levels of flight activity characteristic of the various families are, when allowance is made for the number of species, consistent with Leston's (1957) values for their spread potential.

12. A systematic review is given of the new information provided by the present study on the level of flight activity of various taxa. Closely related taxa often differ greatly, *e.g.* the activity of the Cydnidae as a family is high, of the Pentatomidae, low; that of the genus *Lygus*, high, of *Liocoris*, low; that of *Orthops kalmi* L. high, and of *O. campestris* L. low.

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